



FIGURE 1. *Wallenia yunquensis*. Plant grown from seed in greenhouses of the Arnold Arboretum. Short shoots, or terminal rosettes of leaves, and the single unit sympodial branching are all shown.

were further affected by the development of lateral branches. *Wallenia yunquensis* commonly exhibits a vertical shoot producing a single lateral flush of growth as a branch (FIG. 1). The erect main shoot of *Wallenia*

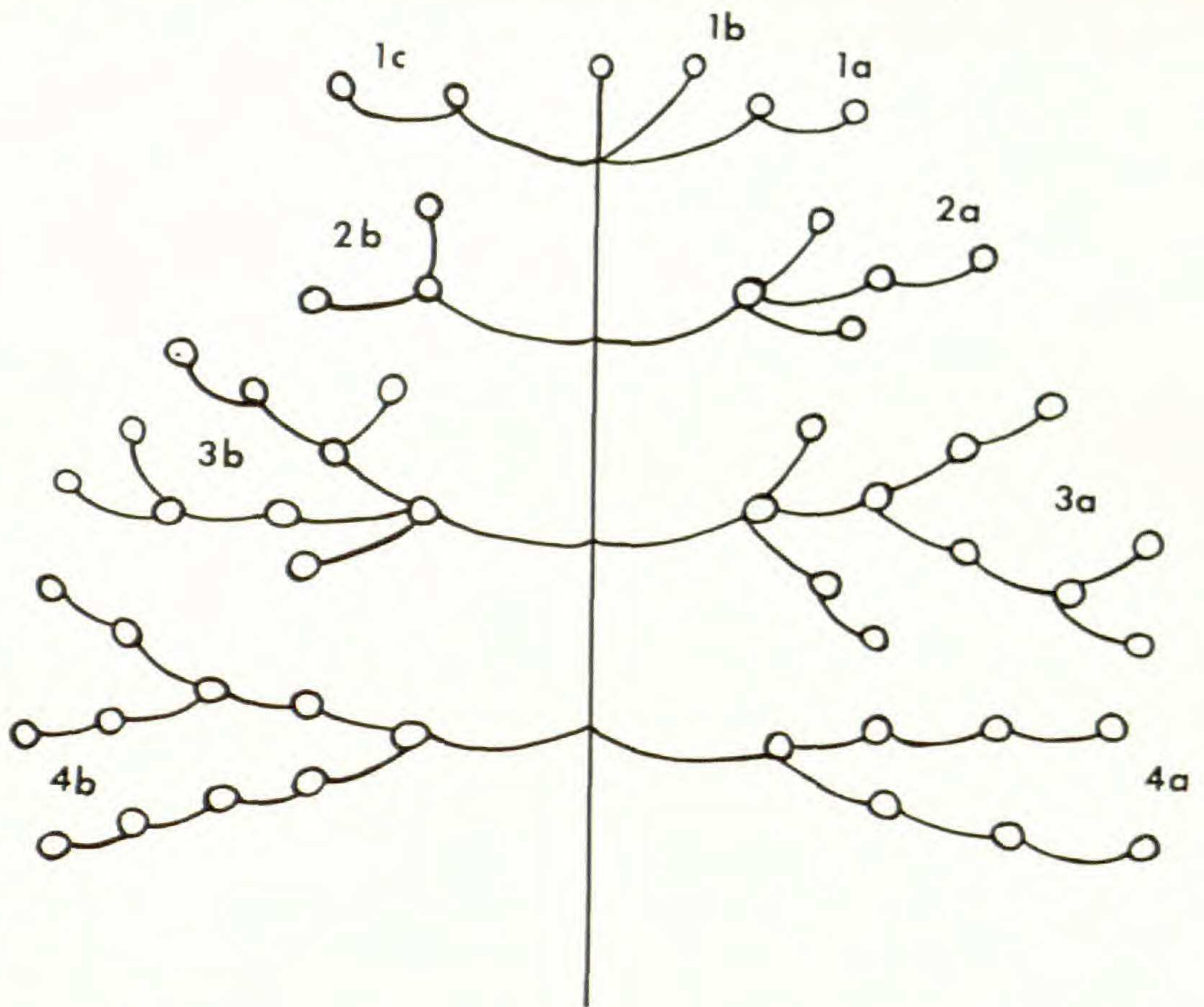
may be interrupted by short shoot areas separated by areas of long shoot development. From one or more leaf axils in the short shoot zone a single fast-growing lateral branch may develop which appears naked at the base but does in fact have widely separated cataphylls of very short duration. The naked shoots are terminated with a short shoot zone possessing an aggregate of leaves. The lateral branch may also originate from the area of cataphylls. In *Wallenia* the lateral flush shoots never branched or continued growth beyond the initial flush.

An example of repeated sympodial lateral branching is readily seen in *Ocotea spathulata*. The development of flush shoots appeared to be from a short shoot zone in all cases, but there developed additional and comparable lateral shoots from the terminal short shoot zone of the lateral branch. This growth pattern results in a sympodial development of lateral branches in a flat plane. The principal branches are tiered in appearance, the tiers being separated by an unbranched, seemingly naked stem. This growth form has been described as candelabra-branching, Terminalia-branching, or as pagoda trees.

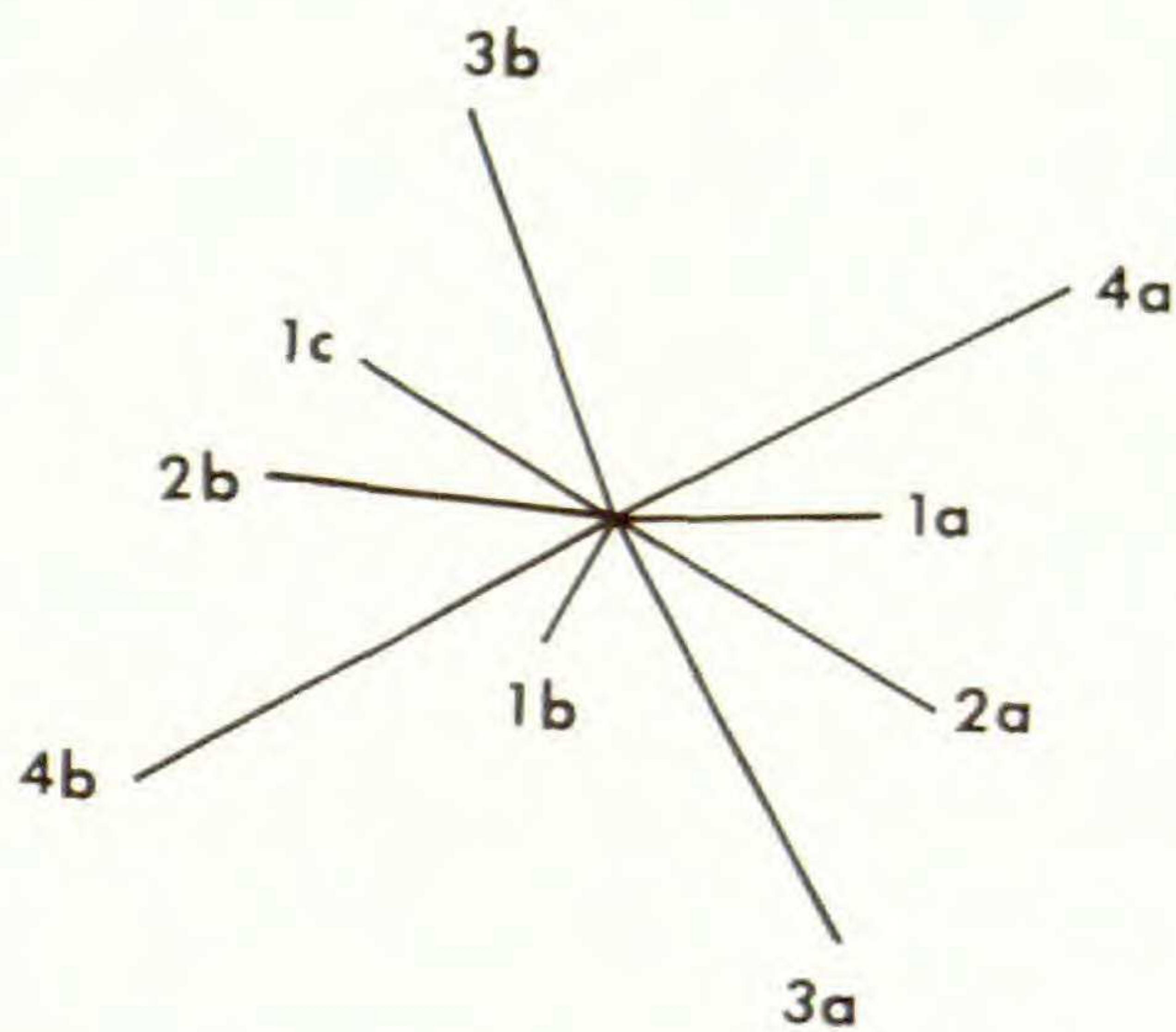
Corner (1952, p. 32) described this growth pattern for *Terminalia* as follows: "The leader-shoot rather suddenly lengthens into a long vertical finger clothed with a lax spiral of leaves . . . its growth slackens . . . and . . . another terminal rosette is produced. From the base of this rosette several twigs grow out to form the next tier of branches . . . The positions of the branches in successive tiers usually alternate so that only those of every other tier are superimposed."

Lateral branches from the terminal short shoot area may also grow vigorously, producing scales or cataphylls before developing normal leaves and, ultimately, each its own terminal shoot. Corner (1952, p. 31) described the lateral growth as follows: "Each twig which grows from the leader-shoot of the tree does so rapidly and at a wide angle from it; then, as its growth slackens, it turns up at the end and from its lower side, just at the bend, a branch arises to grow out as another twig which will follow the same course by turning up at the end and branching in its turn . . . In the first horizontal part of such a twig the internodes are lengthened; the leaves, or their scars, are widely spaced on the slender stem; and the growth has been rapid so that the new shoot has quickly been thrust beyond the parent rosette of leaves. In the second, vertical or upturned, part of the twig the internodes are very short or absent and the leaves, or their scars, are very crowded on a stout stem so that, while many more leaves are being produced than in the previous stage of the twig's development, its growth in length is much retarded: eventually the twig ceases growing, withers and falls off. When such a limb . . . is growing out from the trunk of the tree, it diverges from its neighbours and begins to branch sideways: this it does by producing every now and again not one twig but a pair of twigs, or even three, which grow out from each other at a wide angle; and thus the limb develops into a fan-shaped leafy spray."

The Terminalia-type of branching was particularly conspicuous in *Ocotea spathulata* (Lauraceae), one of the dominant trees of the elfin forest.



A



B

FIGURE 2. Diagram of growth pattern of *Ocotea spathulata*. A, side view showing tiers of repeated sympodial branching; B, view from above showing the relationship of the tiered branches. Drawing by Pamela Bruns.

FIGURE 2A shows, diagrammatically, a plant of *Ocotea* of average stature in the forest with four tiers of sympodially developed lateral branches. It is evident that the terminal growth is impeded while the lateral sympodial growth proceeds. Lateral branches at 4a or 4b show four additional flushes of growth while only 3 periods of reactivation of the terminal shoot are evident. The lateral branches, 1a and 1c, have each had one reactivation of growth while the terminal remains static. The relationship of the lateral branches is illustrated in FIGURE 2B and shows a conflict with Corner's observation that the branches of alternate vertical flushes are superimposed.

Specimens of *Ocotea* were found within the elfin forest with 27 flushes of sympodial lateral growth on the oldest branch. Only the last 13 of these sympodial flushes retained any foliage demonstrating a die-back of the upturned short shoot after a considerable period of continued lateral sympodial growth.

Terminalia-branching was also observed in *Ardisia* and *Grammadenia* (Myrsinaceae), in *Torrabasia* (Celastraceae), and in *Calycogonium* (Melastomataceae). Terminalia-branching is conspicuous in *Hedyosmum arborescens* and is due to the naked areas of elongation and the terminal production of leaf pairs or of an inflorescence. Continued growth of the sympodial branches in this species was restricted in many examples by the production of an inflorescence.

The sympodially branched lateral shoots can develop vertical extensions as well as horizontal branches. Vertically developed shoots as elongate leaders of vigorous growth have been observed on the lateral branches of specimens of *Ocotea* and *Calycogonium*, but in all cases additional sympodial branching also occurred from the same upturned short shoot and beyond it.

Attempts were made to induce either vertical elongation of the upturned shoot or the production of new or additional sympodial branching by pruning the leader shoot. During the three year time interval of the study all of the branches which had been pruned of lateral growth failed to respond by any new development from the areas of the upturned shoot. Likewise, vertical leaders when partially or completely decapitated by pruning failed to develop any sympodial lateral branches.

Although many branches were marked along the trail to record growth phenomena, we were unable to draw conclusions on the frequency with which sympodial branching occurred normally. In no case where sympodial branching was noted in early stages of development (and the branch tagged for observation) was there any further sympodial branching. We could only conclude that the sympodial branches were *not produced annually* on any branch we had marked for observation.

Gill has reported the occurrence of adventitious or aërial roots on the species within this forest. Although adventitious roots were observed on the horizontal branches of the species exhibiting sympodial lateral branching, the roots did not appear to be associated with the short shoot area or the curved portion of the lateral branch. *Ocotea*, which had the most

conspicuous Terminalia-branching, rarely produced adventitious roots from the horizontal branches but did develop "prop" roots from the base of the stem.

The development of sympodial branching or of vertically continuous long shoot-short shoot growth patterns was not associated with flowering in *Ocotea*, *Grammadenia*, *Torralsasia*, *Calycogonium* or *Wallenia*. *Ardisia*, however, did develop a terminal inflorescence, and following the maturity of the fruit and the fall of the inflorescence axis, a lateral but vertical continuation of the stem developed as a sympodial flush of growth.

### DICHOTOMOUS BRANCHING

The dichotomous branching of upright shoots was observed in a number of the components of the elfin forest. Dichotomous growth and branching was most conspicuous in *Calyptranthes* where it occurred, on the average, every three internodes. The new shoots developed in pairs and normally two pairs of leaves developed in each flush before elongation stopped. At the apex of each shoot there was a terminal aborted primordium. Subsequent branching occurred lateral to the terminal aborted primordia but remained consistently in one plane. *Calyptranthes* appeared to be a collection of upright fans of dichotomous branches.

The three species of *Miconia* always developed upright dichotomous shoots when growth was terminated by the production of a terminal inflorescence. Two lateral buds continued the upright vegetative growth after the inflorescence had matured fruit and had fallen. Subsequent growth consisted of but one or two pairs of leaves per flush. In mature plants flowering followed the maturation of each flush of growth on an annual basis.

In *Eugenia borinquensis* one or two pairs of leaves formed each flush of growth. Flowering occurred only on mature stems and terminated the branch or was formed in an axillary position on the old wood.

Both species of *Psychotria* produced a terminal inflorescence and there was no further vegetative growth on that shoot while the inflorescence persisted. With the maturity and desiccation of the inflorescence, however, two basal axillary buds developed in *Psychotria berteriana*, producing a dichotomous growth pattern. In *Psychotria guadalupensis*, however, only a single bud developed at the base of the inflorescence and the resulting growth was falsely monopodial.

Among the herbaceous vines *Ipomoea repanda*, with alternate leaves, produced a terminal inflorescence of many flowers which matured over an extended period of time. Axillary vegetative shoots often developed while the inflorescence was only partially mature. In *Mikania pachyphylla*, with opposite leaves, a terminal inflorescence appeared to restrict apical growth while the terminal inflorescence matured, but then a dichotomous growth pattern developed through activity of two axillary buds.

The heteroblastic growth of *Marcgravia sintenisii* also showed an association with the production of a terminal inflorescence. Subsequent

growth was by the development of axillary buds below the inflorescence. In all cases observed, leaves of the initial production on this axillary shoot were of the juvenile form whether or not the branch was in contact with a trunk or branch.

Plants of *Tabebuia rigida* formed the second major component of the forest and these plants produced flowers throughout the year mostly from new growth. The terminal flush of growth consisted of an average of two pairs of leaves and several axillary and adventitious flowering branches. Most of the plants of *Tabebuia* which were observed in the canopy of the forest also showed a significant die-back of the flush growth during the winter season. Subsequent apical growth, therefore, came from adventitious buds in the axils of lower leaves or from opposite buds of such a node.

### DIE-BACK

Regular die-back of terminal and, less frequently, of lateral or sympodial shoots was observed in *Ilex sintenisii*, *Cleyera albopunctata*, *Eugenia borinquensis*, *Hornemannia racemosa*, *Ardisia luquillensis*, *Micropholis garciniaefolia*, *Alloplectus ambiguus*, *Gesneria sintenisii* and *Lobelia portoricensis*. Although regular die-back has been described for plants of temperate areas, its occurrence as a factor in the size of a plant in tropical areas has not been recognized previously (Garrison & Wetmore 1961).

Relatively long flushes of shoot development were observed in *Gonocalyx* and *Hornemannia* consisting of 5–10 leaves or internodes per flush. The young leaves were brightly colored and soft until full extension of the shoot, or the full development of the leaf size, was completed. Both species were climbers and the soft shoot development was often injured mechanically and the entire flush of growth abscised.

The height of the forest may be affected by the environmental factors previously suggested, but clearly the low stature of the component woody species may also be due to genetic factors expressed as long shoot-short shoot development, dichotomous branching associated with a terminal inflorescence, the abortion of the shoot tip, and the die-back of seasonal flushes of growth.

Continuous production of single leaves or leaf pairs occurred in all of the herbaceous species in the elfin forest. Continuous production of single leaves or leaf pairs appeared to occur in both juvenile and adult shoots of *Marcgravia*, in *Symplocos*, *Cleyera*, *Ilex*, *Gesneria*, *Clusia*, and *Micropholis*. The herbaceous vines *Rajania*, *Ipomoea* and *Mikania* also appeared to produce leaves continuously unless affected by flowering.

The rosette and epiphytic habit of the two members of the Bromeliaceae found within the elfin forest can be regarded as a family genetic character. Following flowering, however, the two species continued growth in different patterns. Rosettes of both species died following flowering, but plants of *Guzmania* produced one or, rarely, two basal vegetative rhizomes which

developed laterally before terminating into a rosette or crown of leaves. This growth pattern caused the plants to form a ring around the host tree and *Guzmania* was most commonly found on the large trunks of *Prestoea montana*. *Vriesea sintenisii* by contrast, produced a single basal rhizome which tended to grow upward immediately and formed a new crown in close competition with the parent rosette. The new growth could be to the right or the left of the parent plant but always extended upward. Plants with 7 generations of rosette-rhizome vertical development were found. When *Vriesea sintenisii* occurred on a branch extending horizontally, the plants persisted for only 2 or 3 growth generations before being extended slightly off center and, seemingly top heavy, falling over to break free and drop to the ground.

#### BUD PROTECTION

Richards (1952, p. 77) notes that "buds of rain-forest trees and shrubs, as might be expected, are less well protected than those of trees in other climates." An examination of the terminal foliage buds or the shoot apex in resting condition revealed that the leaf primordia are better protected in the plants of the elfin forest than might be expected from Richards' statement. (PLATE I).

Protective stipules are present in *Hillia* and *Psychotria* of the Rubiaceae and in *Calyptranthes* of the Myrtaceae. In *Hillia* (PLATE Ib) the stipules form a sheath around the young leaves which is compressed at the apex. The developing young leaves force an opening in the apex of the sheath. *Psychotria* species have smaller stipules consisting of an ochrea-like base with four short free apices. The apices tend to be closely associated in very young buds but their protective function would be of short duration.

*Calyptranthes* possesses a peculiar type of stipule protection for which we have not found a description elsewhere (PLATE Ig). In fact Berg, in a monograph, reports the family to be estipulate, as have subsequent authors. McVaugh makes no mention of the foliage bud protection. In the original description of *Calyptranthes krugii*, Kiaerskou notes, "Quaque innovatio e duobus internodiis constat, quarum alterum breve duo cataphylla opposita cito decidua, alterum longum duo euphylla fert." In a footnote he equates "cataphylla" with "Niederblätter Germanorum." In our observations of *Calyptranthes krugii* on Pico del Oeste the vegetative shoot increase is by production of 1 or 2 pairs of leaves in a flush. The apical meristem aborts although an inflorescence of one, rarely two, flowers may be produced in one or both terminal leaf axils. Subsequently, after flowering or resting, two axillary shoots develop and in each the apex is covered with a pair of laterally folded bud scales. The young leaves increase in size uniformly and are appressed by their ventral or adaxial surfaces. As the leaves increase in size, the bud covering is forced apart or torn free at the base, and the two halves separate as conduplicate folded sheaths. The bud scales are a light yellow or cream color in contrast to

the green shoots. When separate they dry white, then brown and shrivel before falling from the shoot. Although these bud scales are rarely found on herbarium sheets, they were conspicuous in the living plants of *Calypttranthes krugii* in the study area and were also found on a population of *Calypttranthes* which may represent a different species in the Cerro de Punta area. The term cataphyll although broadly inclusive for the early leaves of a plant or shoot as cotyledons, bud scales, etc. (Jackson) is scarcely descriptive of the folded protective scales of the young leaves of *Calypttranthes*.

Apical buds may be protected by leaf bases as in *Clusia* which has opposite leaves or by the cluster of leaves in the several genera which produce terminal or lateral long shoots where the terminal apical elongation is reduced. In *Clusia* (PLATE If) the mature leaves conceal the young buds as the leaf bases of opposite leaves of a pair are tightly appressed. In *Wallenia*, *Ocotea*, *Grammadenia*, *Torrabasia*, *Ilex* (PLATE Ic), and others, the vegetative shoot in resting condition is terminated by a dense cluster of small leaves or primordia. In subsequent development of the shoot represented by these primordia, the outer ones enlarge only slightly, frequently failing to develop a leaf blade even though the petiole may elongate. Such scales or cataphylls are found at the base of the long shoot and the internodes between them may or may not have elongated. Clearly these cataphylls have served a function of protection for the inner leaves and the apical meristem.

The buds or apical meristem of shoots of *Hedyosmum* are enclosed within the sheathing stipular base of the leaves (PLATE Ie). Bud protection here is evident in the enclosure of the primordia in the sheathing leaf base.

The apex of the stem of *Micropholis* and *Symplocos* have the young leaf primordia tightly invested in a protective covering of brown trichomes. As the leaves expand these trichomes are separated and in many cases break off. In *Tabebuia rigida* the young leaves or primordia are tightly and completely encased in a shield of brown peltate scales. Again with leaf enlargement the scales are separated and often persist in isolated positions on the mature leaves.

The species *Gesneria sintenisii* appears to have a large naked meristem where the leaf primordia are separated and evident from an early age (PLATE Id). The leaf primordia and the apex of the stem have a dense resinous covering. As the leaf starts to expand the resinous covering is cracked and usually flakes off although sections of the covering may persist even on the mature leaf blade and the petioles.

The young leaves of *Marcgravia* (PLATE Ia) and *Cleyera* are convolute in bud and appear to unroll in development. The apical meristem is enclosed within this pointed bud and the youngest leaf primordia do receive some protection.

It is clear from these examples that the young leaves are not without protection in the majority of the species that comprise the woody components of the elfin forest on Pico del Oeste.



## LEAF SIZE AND MORPHOLOGY

Plants of tropical forests have been grouped on the basis of leaf size: dimensions and areas. Raunkiaer proposed a classification of life forms on leaf-size classes which has been used for comparison and description by many authors. Leaves have been termed leptophylls if their area does not exceed 0.25 cm.<sup>2</sup>; nanophylls if their area is between 0.25 and 2.25 cm.<sup>2</sup>; microphylls if the area is 2.25–20 cm.<sup>2</sup>; mesophylls if the leaf area is 20–182 cm.<sup>2</sup>; and macrophylls if the area is 182–1640 cm.<sup>2</sup> Cain *et al.*, found, in a Brazilian rain forest, that the phanerophytes are strongly mesophyllous and reported a tendency for the small leaf size classes to have a higher percentage in taller strata than in lower ones.

Brown, in his study of the mossy forest on Mount Maquiling in the Philippines, found only the leaf-size classes of microphyll and mesophyll represented in approximately the same numbers.

The elfin forest on Pico del Oeste had a single species (*Peperomia emarginella*) of a size class smaller than the nanophyll classification and the majority of plants were of the microphyll size class. The total classification in numbers of taxa and percentage of the totals is the following:

leptophylls	1	1.9%
nanophylls	6	11.5%
microphylls	30	57.6%
mesophylls	13	25.0%
macrophylls	2	3.8%

Compound leaf types were represented only by *Trichilia pallida*, a species clearly only surviving and not reproducing in the elfin forest zone. At lower elevations *Trichilia pallida* becomes a small tree while most of the plants found on Pico del Oeste were weak saplings, dependent for support on the surrounding vegetation and nearly scrambling through the elfin forest. A single plant of *Weinmannia pinnata* (Cunoniaceae) with compound leaves was found on the peak but was not encountered in the transects. Brown did not have a compound-leaved plant in the Philippine study area and Lebrun notes such plants are less than 15% in African elfin forests.

The largest leaves, macrophylls, were those of *Prestoea montana*, a palm, restricted to the leeward erosion valleys and *Anthurium dominicense*, an epiphytic member of the Araceae.

When grouped according to habit the following leaf-size classification was obtained:

LEAF SIZE	VINES-SCRAMBLERS	HERBS	EPIPHYTES	TREES & SHRUBS
leptophylls	0	1	0	0
nanophylls	1	2	2	1
microphylls	3	10	2	15
mesophylls	1	2	2	8
macrophylls	0	0	1	1

Brown added data on leaf dimensions and leaf margins to his study of the Mt. Maquiling forest in the Philippines. He found the leaves were

0–10 cm. long in 11 species or 70%, and 10–20 cm. long in 5 species or 30% of the plants. The leaves were 0–5 cm. wide in 12 species or 75%, and 5–10 cm. wide in 4 species or 25%.

In the elfin forest of Pico del Oeste the leaves were 0–10 cm. long in 7 species of monocotyledons and 31 species of dicotyledons or 70% of the total flora; and 10–20 cm. long in 7 species of monocotyledons and 9 species of dicotyledons or 30% of the total. The leaves were 0–5 cm. wide in 10 species of monocots and 33 species of dicotyledons or 79%, and 5–10 cm. wide in 4 species of monocotyledons and 7 species of dicotyledons or 21%. The leaves selected for these measurements were taken from the mature growth and were averaged for the plant. Variation in leaf size within a given plant ranged from the cataphylls and reduced leaves of initial growth of long shoots to the larger leaves of vegetative shoots, when compared with those of flowering branches. Heterophylly was found in dimorphic pairs of leaves in *Pilea krugii*, *Pilea yunquensis* (Urticaceae) and in *Alloplectus ambiguus* (Gesneriaceae). Heteroblastic growth was found only in *Marcgravia sintenisii* with appressed smaller leaves on juvenile and climbing shoots and larger leaves on the free arching branches. Heterophylly with age was observed in *Ocotea spathulata* and *Symplocos micrantha* where the leaves of seedling plants appeared to be quite different in size and shape from those of adult plants. Although *Cleyera albopunctata* appeared to have larger than average leaves on some vigorous growing branches this could not be documented with measurement of samples. However, the leaves of sterile or vegetative branches of *Clusia grisebachiana* did possess larger leaves than were found on shoots which were mature or produced inflorescences. Macrophyly on adventitious shoots was not encountered within this forest.

Much attention has been given in existing studies of tropical forests to the shape of the leaf, the nature of the margin, apex and base of the blade, and to the presence of a cuticular layer in relation to the retention of water or the presence of epiphyllous organisms.

Brown noted in his study of the mossy forest at 1000 meters in the Philippines that as the altitude increases there is a marked increase in the percentage of small leaves and a decrease in the percentage of leaves with entire margins. It has been suggested that the presence of marginal teeth aids the runoff of water from the leaf surface, and Brown found entire leaves in eleven species of Philippines plants in the study area and five species in which the margin was not entire. In Puerto Rico on Pico del Oeste 29 taxa had entire leaves while eleven taxa of dicotyledonous plants had leaf margins with coarse or blunt teeth or with marginal undulation.

The extended leaf tip, often called a drip-tip, has a popular association with wet tropical forests. The conclusion of Junger has been cited repeatedly that the function of the pointed leaf tip was to hasten the runoff of water from the leaf, and thus help prevent insects and lower plants from attacking them. Baker recorded 37 of 41 species of plants belonging to 20 families with leaves drawn out into a tip, in a forest in Ceylon, and

Richards observed, "Pointed tips to leaves are characteristic of plants of wet regions and especially of tropical rain-forests, but I doubt whether any rain forest can show the phenomenon more markedly than the Sinharaka." Richards observed that drip tips are common and better developed in the lower than in the upper strata of the forest and in juvenile than in mature leaves of tall trees. Cain *et al.* reported that 70.6% of the leaves in the Brazilian forest they studied had acuminate tips and 28% of the 150 species studied had rather abruptly long tips of the drip point type.

By contrast, Shreve found drip tips uncommon in the montane rain forest of Jamaica, and Vaughan and Wiehe reported a similar observation for upland climax forest of Mauritius.

In the Pico del Oeste forest 13 of the 14 taxa of monocotyledons had the leaves acuminate at the apex and the other taxon had leaves acute. Among the dicotyledonous plants the apex could be classified as acuminate in 15 taxa of which 6 would qualify as drip tips; 14 taxa had the leaves acute at the apex and 11 had the leaves obtuse, blunt, or emarginate.

Although previous authors have not considered the leaf base, it seems that if leaf shape is important for drainage in one direction, it is equally so in the other. Only 5 of the 14 taxa of monocotyledons have petioles and of those, *Prestoea montana*, the mountain palm, has lacerate or compound leaves; *Rajania cordata* and *Anthurium dominicense* have the basal lobes extended and *Renealmia antillarum* and *Brachionidium parvum* have the leaf base obtuse. Of the dicotyledonous plants 24 taxa had the leaf base blunt, acuminate, or decurrent on the petiole while 16 are best described as cordate to peltate at the base.

All of the leaves which were cordate, hastate, or peltate at the base had an acuminate apex or a drip tip. All leaves which were blunt at the apex or rounded or emarginate had acute or decurrent leaf bases except for *Micropholis garciniaefolia* and *Eugenia borinquensis*. In these two taxa the attitude of the leaves to the stem tended to be either upright or drooping and in this manner adapted to the runoff of water. Excepting *Eugenia*, those leaves with short petioles or with petiole:blade ratios 1:10 or larger, all had tapering blade bases with the leaves mostly arranged upward in attitude. *Cleyera albopunctata* has short petioles but the leaves have a noticeable curvature. *Marcgravia sintenisii*, again with a short petiole, also has a slight curvature and a drip tip.

The frequency of taxa having leaves of strongly curved form suggests a selective value can be attached to this growth form. The blades may be noticeably curved longitudinally as well as laterally or in but one plane. This curved form is particularly evident in taxa of *Calycogonium*, *Cleyera*, *Gesneria*, *Gonocalyx*, *Hornemannia*, *Ilex*, *Miconia pycnoneura*, *Symplocos*, *Tabebuia*, and *Torrabasia*, that is in 10 of the 40 taxa of dicotyledons or 25% of the flora.

A heavy upper cuticle was found in 22 taxa or 55% of the dicotyledonous plants. *Ardisia*, *Cleyera*, *Clusia*, *Calyptranthes*, *Calycogonium*, *Eugenia*, *Gonocaylx*, *Haenianthus*, *Hillia*, *Hornemannia*, *Ilex*, *Marcgravia*,

*Miconia foveolata*, *Miconia pachyphylla*, *Miconia pycnoneura*, *Micropholis*, *Ocotea*, *Psychotria guadalupensis*, *Symplocos*, *Trichilia*, *Torrabasia*, *Tabebuia*, and *Wallenia*, that is, all woody taxa except *Mecranium amygdalinum*, *Grammadenia sintenisii*, *Hedyosmum arborescens* and *Psychotria berteriana* possess a heavy upper cuticular layer.

Junger found that leaves with drip tips were less frequently overgrown with algae, fungi, lichens and bryophytes than those without. He believed that the presence of these epiphyllae interfered with assimilation to such an extent as to be a serious handicap to the plant. *Micropholis garciniaefolia* and *Eugenia borinquensis*, which stand out as the only taxa of the 40 dicotyledons or 29 woody plants in which the leaves were rounded or cordate at the base and rounded at the apex and appear to lack any special adaptation for getting rid of surface water, seemed to support the larger populations of epiphyllous plants. The abundance of epiphyllous leafy Hepaticae on different species will be considered later in this paper in relation to the metabolism of the forest.

In a superficial classification of the texture of leaves within the forest components, the leaves would be considered as membranaceous in all of the monocotyledons except *Anthurium*, which had leathery leaves. Among the dicotyledonous plants 13 taxa would have the leaves classified as membranaceous, 8 taxa would be described as fleshy or succulent, and 21 taxa as having the leaves leathery or coriaceous. The high percentage of water in the tissues or the relatively small amount of material forming dried weight will be considered later and is indicated in TABLE 1, column 8.

The heavy texture of the leaves, the thickness of the blade, and the amount of succulence all support previous suggestions that the flora of the mountain summit shows many xeromorphic characteristics. Bews regards the rain forest type of leaf as xeromorphic and associates its characters with the low specific conductivity of the wood for water. Shreve remarks that the prolonged occurrence of rain, fog, and high humidity at relatively low temperatures places the vegetation of a montane rain forest under conditions which are so unfavorable as to be comparable with the conditions of many extremely arid regions. Xeromorphy is usually interpreted from such anatomical characteristics as cuticle, hypodermis, thin palisade layers, pubescence or idioblasts.

Wylie (1954) noted that a xerophytic flora may have a high proportion of representatives with leaves having a hypodermis. In his studies of plants of North Island in New Zealand, Wylie, even though avoiding "extreme xeromorphs and succulents," concluded that the species studied revealed a high average thickness of leaves, extensive spongy mesophyll and palisade parenchyma areas, great cuticular depth, and "the proportion having a hypodermis were greater than for any group previously studied." Wylie (1946) compared his studies of the New Zealand plants with previous ones of his own, based on plants of Florida and of other temperate areas.

Wylie reported that the leaves of the New Zealand species studied, ranged in blade thickness from 731  $\mu$  for *Pseudopanax* to 172  $\mu$  for *Olearia*,

and the 38 species averaged  $406 \mu$ . This was much greater than the corresponding thickness of  $216 \mu$  for 121 Florida dicotyledons and  $80 \mu$  for 80 species of northern dicotyledonous trees. Philpott reported a mean blade thickness of  $234 \mu$  for 24 species of *Ficus* growing in Florida and Cooper found a mean laminar thickness of  $336 \mu$  for 19 species of woody dicotyledonous plants in the climax chaparral in western California.

Within the Pico del Oeste forest the woody plants by comparison had leaves ranging in thickness from  $787 \mu$  in *Clusia grisebachiana* to  $146 \mu$  in *Psychotria berteriana* and averaged  $379.6 \mu$  in thickness. The herbaceous flora had leaves ranging in thickness from  $625 \mu$  in *Peperomia hernandii-folia* to  $141 \mu$  in *Sauvagesia erecta*, and all herbs had leaves averaging  $281.6 \mu$  in thickness (TABLE 2, column 1).

Wylie reported that a hypodermis was found in 24 or 63% of the 38 species examined in the New Zealand study area. Eighteen species had a hypodermis on both the upper and lower surface, 5 species had only an upper hypodermis, and one species is described as having only a hypodermis on the lower side.

In the Pico del Oeste elfin woodland 19 of 40 taxa or 47% have a hypodermis. Two taxa, *Begonia decandra* and *Hillia parasitica* had both an upper and a lower hypodermis. No plant was observed with only a lower hypodermis. Seventeen taxa had an upper hypodermis alone. Twenty-one taxa did not possess a hypodermis (TABLE 2, columns 2, 3).

The presence of a hypodermis is often regarded as a xeromorphic character, although a multiple hypodermis is also an anatomical characteristic of taxonomic value. Carlquist noted that "continued periclinal division of the epidermis is of taxonomic importance in certain families such as the Piperaceae." Within the plants of Pico del Oeste, multiple hypodermal layers were found in taxa of *Peperomia* (Piperaceae), *Hedyosmum*, (Chloranthaceae), *Ocotea* (Lauraceae), *Clusia* (Guttiferae), *Calycogonium* (Melastomataceae), and *Hornemannia* (Ericaceae).

A ratio was determined between the thickness of the upper epidermis and that of the upper hypodermis in this mossy forest. Ratios varied from 1:1 in most plants with a hypodermis, to 1:15 in *Psychotria guadalupensis* and averaged 1:4.1. Although Wylie did not use such a figure calculation, the figures in table 2 of his paper (1954) suggest a ratio range in the New Zealand plants from 11:1 to 1:21.3 but an average of 1:3.8, or less than that found in the Puerto Rican vegetation.

Stålfelt considers the mechanical strengthening of leaves through the development of sclerenchyma as particularly common among xerophytes as a means of reducing the injurious effect of wilting. Branched idioblasts were found in but four taxa within the mossy elfin forest (TABLE 2, column 8 and PLATE IIa).

Watson concluded that the formation of palisade tissues in leaves might be a morphological response to light. He suggested that the cigar-shaped palisade cells are formed in increasing number with increasing light intensity during leaf development. We examined the leaves on Pico del Oeste to see if palisade mesophyll development was reduced with the re-

duced light intensities we have reported there (Baynton 1968, 1969). Two taxa, *Lobelia portoricensis* and *Mikania pachyphylla*, seemed to be without a definite palisade layer in the leaves examined (PLATE II d). Further, 19 of the remaining 38 taxa possessed a palisade mesophyll of but a single cell in thickness. The remaining 19 taxa had a palisade mesophyll in part exceeding a single cell layer to 3 to 4 cells in thickness (TABLE 2, column 9). In taxa which could be measured, the palisade layer exceeded the spongy layer in thickness in only 4 taxa, while the ratio of palisade to spongy, in 34 taxa, ranged from 1:1 to 1:7.4 and averaged 1:2.4 (TABLE 2, column 10). Referring to Wylie's study of New Zealand plants, of the 38 taxa he examined 7 had a thicker palisade layer than spongy layer and the comparable ratios determined from the figures he gave show a range from 1:1 to 1:3.3 with an average of 1:1.5.

On the basis of limited comparative data it appears that the leaves of the plants growing in the elfin forest on the summit of Pico del Oeste are thicker than usual and approach leaves of admittedly xeromorphic type. The frequency of a hypodermal layer or multiple hypodermal layers is high. The ratio of thickness of palisade and spongy mesophyll layers suggests that the plants surviving on Pico del Oeste have adjusted to the low light values through a reduction in the palisade mesophyll zone and an increase in the amount of spongy mesophyll.

#### LEAF DEVELOPMENT

Richards has reviewed the earlier literature which claimed that a few species in Buitenzorg were ever-growing and showed no foliar periodicity whatever. On further study it was shown that one plant at least was in continuous leaf production when young, but when older leaf production was distinctly periodic. Richards (1964, p. 193) concluded that "it is certainly true that most rain-forest trees produce new leaves, not continuously, but in periodic flushes, so that a single shoot bears several 'generations' of leaves at the same time."

Our observations on the development of stems were in relation to the production of leaves (TABLE 3). Initially we observed that certain plants did grow in obvious flushes where the young leaves were brightly colored or soft in texture in comparison with the mature leaves. We recognized 20 taxa which grew in flushes, 8 of which had conspicuous terminal long shoot-short shoot growth patterns. Twelve taxa were considered to be in continuous production of leaves but this varied from branch to branch on a given plant. A large specimen of *Clusia grisebachiana*, for example, failed to produce a single new leaf during the period of this study. A marked plant of *Trichilia pallida* did not add a single leaf, or lose any, for a period of three years after the plant was tagged for observation. *Ilex sintenisii* which appeared to have young green leaves all of the time proved to have only some of the individual shoots on the plant in a stage of growth or expansion at any given time. A shoot of *Ilex* tagged for observation was shown to produce a flush of leaves and then remain in a mature

but quiescent stage before renewing its growth. Some of the shoots renewed growth with no change in the size of the leaves while others had an initial renewal of growth in the production of leaves, or a single leaf of smaller size or reduced to cataphyll proportions. When the internodes along a stem were measured carefully there was evidence that growth of the internodes had been reduced in some areas giving further evidence to a periodicity of growth.

Clearly, it is difficult to determine that a given shoot has not added a leaf, but the majority of plants observed in the elfin forest did exhibit some degree of periodicity of growth and leaf production during the period of study.

The suggestion has been made that leaves develop quickly in tropical forests. Studies of leaf expansion within a temperate area at the Arnold Arboretum in Boston have indicated that leaf expansion takes place within a 10-day to three-week period in most native and cultivated species. Although many species studied within the elfin forest did complete the expansion of leaves within that period, there were notable exceptions. Tagged shoots where fairly large leaves were counted and observed at regular intervals showed the following times for development from a noticeable leaf primordium to full expansion.

<i>Symplocos micrantha</i>	5 weeks
<i>Clusia grisebachiana</i>	7 weeks
<i>Hedyosmum arborescens</i>	6-8 weeks
<i>Calycogonium squamulosum</i>	8 weeks
<i>Gesneria sintenisii</i>	10 weeks
<i>Miconia pycnoneura</i>	14 weeks

#### NUMBER AND PERSISTENCE OF LEAVES PER PLANT

Regular observations of the elfin forest components impressed upon us the fact that some plants had many leaves and that others, equally characteristically, had few leaves. Although the leaves may have been produced in flushes of growth or seemingly continuously, there was a leaf fall that in most plants seemed to equal leaf production. We selected 24 plants of comparable size and age of *Miconia pachyphylla*, *Wallenia yunquensis* and *Dilomilis montana*, counted the leaves, and found less than 5% variation in the number of leaves on a given plant of the species. Branches of *Miconia foveolata* or *Psychotria berteriana* characteristically had but 3 pairs of leaves at the end of a shoot. When new growth occurred the new shoot had a comparable number of leaves and the leaves of the former growth generation abscised. The largest number of leaves on a mature plant was found on *Micropholis garciniaefolia* with 10,487, while *Brachionidium parvum* characteristically had but 4 leaves per plant.

The following table indicates the plants with the greatest number of leaves in comparison with the total photosynthetic area represented on the plant, and the rank of the plant in frequency counts for transects reported in the first paper of this series. Leaf numbers and total photosynthetic area for all species is given in TABLE 1. The leaf count was obtained as a

by-product of gathering foliage material for a chemical survey of the plants within the elfin forest.

		TOTAL		
TOTAL NUMBER OF LEAVES		PHOTOSYNTHETIC AREA		FREQUENCY *
<i>Micropholis</i>	10,487	<i>Prestoea</i>	289,460 cm. <sup>2</sup>	<i>Pilea krugii</i>
<i>Ilex</i>	8,684	<i>Micropholis</i>	96,480	<i>Wallenia</i>
<i>Calyptranthes</i>	4,539	<i>Tabebuia</i>	60,040	<i>Calycogonium</i>
<i>Tabebuia</i>	2,680	<i>Hedyosmum</i>	44,908	<i>Vriesea</i>
<i>Hedyosmum</i>	2,339	<i>Eugenia</i>	23,000	<i>Ocotea</i>
<i>Calycogonium</i>	1,345	<i>Lobelia</i>	20,300	<i>Calyptranthes</i>
<i>Ardisia</i>	1,857	<i>Calyptranthes</i>	18,609	<i>Pilea obtusata</i>
<i>Gonocalyx</i>	1,345	<i>Psychotria</i>	18,093	<i>Dilomilis montana</i>
		<i>berteriana</i>		
<i>Haenianthus</i>	1,294	<i>Haenianthus</i>	17,339	<i>Miconia pachyphylla</i>
<i>Marcgravia</i> (adult)	1,280	<i>Ardisia</i>	17,458	<i>Tabebuia rigida</i>
<i>Cleyera</i>	678	<i>Ilex</i>	15,631	<i>Eugenia borinquensis</i>

\* Frequency = descending order of frequency in transects.

Holtum noted that in the uniform climate of Singapore, trees of a number of deciduous species change leaves annually, many in February, others in August, apparently because of leaf senescence.

Within the elfin forest of Pico del Oeste the greatest noticeable leaf fall in the dominant plants of the forest occurred in February for *Eugenia*, *Ocotea*, and *Tabebuia* and was conspicuous in March for *Lobelia*. In each of these plants the leaf fall preceded the development of new year's growth, and the plants presented a barren appearance for a short period in contrast to their normal condition. Other species developed new growth before the erratic abscission of the older leaves.

Richards notes the many widely different types of behavior among tropical trees in regard to leaf fall and leaf persistence. According to Warming and Graebner the average length of leaf life of tropical species is about 13-14 months. We made an attempt to mark branches and to record the number of leaves, the nature of the new growth, and the length of time individual leaves persisted (TABLE 3). In general, the results were unsatisfactory. Often the tagged branch failed to develop any new leaves during the period of observation, while an adjacent branch of the same plant for which data had not been recorded produced a flush of leaves, or flowered, or died. It is not possible to report with accuracy that the growth flush in a long shoot-short shoot growth pattern represented an annual increment of growth as may be done in temperate areas with deciduous or bud-forming plants. We did observe that some leaves remained on the plant during two full years of observation. Branches of *Ilex sintenisii* which appeared to have two flushes of leaves per year retained some leaves through 20 internodes, which represented 7 flushes as determined by areas of short internodes and by cataphylls. *Torralsia cuneifolia*, which also grows in flushes with the production of many cataphylls, also retained leaves for 20 nodes representing 7 flushes in this plant. Only one or two of the larger leaves persisted while cataphylls and



smaller leaves abscised. *Gonocalyx* produced 3 to 4 leaves per flush and retained 20 leaves in 5 recognizable flushes with all leaves persisting. *Tabebuia* tended to retain only 1 pair of leaves of each flush of 2 pairs and the oldest persisting leaves were 10 internodes below the apex, suggesting that some leaves have persisted for five years.

In general, younger plants in the undergrowth tended to hold more leaves per shoot for a longer period of time than did the plants with shoots exposed in the canopy.

#### FACTORS OF PRODUCTIVITY OF THE LEAVES

Although it has been suggested that the persistent cloud cover, high humidity saturated soil, and the growth form of individual plants all influence growth rate or development of the forest, we found additional factors worthy of mention.

The very slow growth of some component trees within the elfin forest has been recorded by Wadsworth and Bonnet in their comparative study of the tabonuco (*Dacryoides excelsa*) rain forest and the colorado (*Cyrilla*) forest in Puerto Rico. Although *Cyrilla racemiflora* was not encountered in the elfin forest of Pico del Oeste, four other taxa of the colorado forest were. No distinctive growth rings have been seen in the woody trunks of the Pico del Oeste plants. Wadsworth and Bonnet grouped the trees in diameter-size classes and estimated the age of the trees by summing the period required for a plant to pass from one diameter class to another. They concluded that a 4" trunk of *Ocotea spathulata* was 200 years old; one of *Micropholis garciniaefolia*, 170 years old; and one of *Calycogonium squamulosum*, 80 years old. The annual growth rate for saw timber and polewood species in the Luquillo Mountains was 0.07 inches for *Tabebuia rigida*, 0.05 inches for *Micropholis garciniaefolia*, and 0.04 inches for *Calycogonium squamulosum* and *Ocotea spathulata*. They concluded that the soil is the common factor most important in the forests they studied. The saturated, poorly aerated organic soil inhibited root penetration and the absorption of water and resulted in the very slow growth.

The cloud and fog cover, the high humidity and abundant rain documented by the studies of Baynton suggest that photosynthetic activity in the elfin forest is low. We were unable to test the amount of photosynthesis carried on by the component species. Tests of evaporation with potometers and of transpiration with cut branches within the forest were complete failures. Gates, however, demonstrated by infra-red temperature measurements that transpiration did occur during brief periods of sunshine and clear sky. As there were longer periods, even days of full sunshine on the peak, the plants grew even though the growth rate was slow.

A survey was made of the stomatal types, size, and distribution to determine any specializations that might occur within the elfin forest components (TABLES 3, 4). Sinnott suggested that xerophytes tend to have a high stomatal frequency but cites no reference. Regrettably, we have failed to find any comparative data for other forest zones.

Although stomatal apparatus types are commonly associated at the family level, there are variations and exceptions as reported throughout the work of Metcalfe and Chalk. We found the anomocytic type of stomatal apparatus (PLATE IIIa) to be most common as represented in 16 taxa of dicotyledons and 4 taxa of monocotyledons. The paracytic type (PLATE IVa) was present in 13 taxa of dicotyledons and 3 monocotyledons. Anisocytic type (PLATE IIIc) was present in 9 taxa of dicotyledons. The gramineous type (PLATE IVd) was present in all 6 taxa of Cyperaceae and Gramineae. A didymocytic stomatal apparatus (PLATE IIIb) was represented in 1 taxon of monocotyledons and 1 of dicotyledons (TABLE 3, column 9; TABLE 4, column 3).

Stomatal openings of varying sizes were found in *Justicia martinsoniana* where large numbers of the stomatal apparatus appeared to abort before the final cell division which, we suspect, would have formed the guard cells. The openings, therefore, were of varying sizes. *Pilea krugii* (PLATE Va) also had stomatal apparatus of varying size with very small guard cells approximately 0.002 mm. long appearing over the veins, while mesophyll tissue was surmounted by guard cells averaging 0.023 mm. in length. *Marcgravia sintenisii* with heteroblastic growth showed the same number of stomata per square mm. for juvenile and adult foliage, but the guard cells were 0.037 mm. long on the juvenile leaves and only 0.028 mm. long on the adult leaves. The stomatal apparatus, however, appeared to be broader in the adult leaves.

Stomata occurred in definite patterns in many of the monocotyledons, as expected, but they were found in groups of 2 to 3 or 3 to 7 in *Grammadenia* (PLATE Vb) and in groups of 6 in *Gesneria sintenisii* and with 2 to 3 very closely associated, almost united, in *Sauvagesia*.

On leaves of *Pilea yunquensis* stomata were found only on the upper surface of the leaf. Metcalfe and Chalk refer to work of Mohler, who found stomata on the lower surface in the species of *Pilea* he examined except for *Pilea spruceana*, where they were on the upper surface. Stomata tended to be oriented around the long hairs on *Cleyera*.

Accessory or subsidiary cells to the guard cells were usually clearly defined and commonly contrasted with those of the epidermis. Unusually shaped subsidiary cells appeared in *Alloplectus* (PLATE IIIc) and in *Justicia martinsoniana* and in *Renealmia antillarum* (PLATE IIIId).

The subsidiary cells had a characteristic homogeneous yellow-brown pigmentation in *Clusia* in contrast to the adjacent epidermal cells. In *Tabebuia rigida* the subsidiary cells were generally clear in contrast to the mottled appearance of the epidermal cells. The walls of the subsidiary cells of *Micropholis* were straight in conspicuous contrast with the sinuous walls of the other epidermal cells.

No conspicuous elevation of stomatal apparatus was discerned in the components of the elfin forest. *Torrabasia* was the only taxon with the guard cells noticeably sunken and overlain by 6 epidermal cells (PLATE IVc).

The length of the guard cells was measured and those found in 14 taxa

of monocotyledons averaged 0.035 mm. in length while in 39 taxa of dicotyledons the guard cells averaged 0.028 mm. in length. Within the monocotyledons the largest guard cells were in *Eleocharis*, measuring 0.048 mm. long, while *Isachne* had the smallest, 0.023 mm. long. Within the dicotyledons the longest guard cells were found in *Hedyosmum arborescens* and *Peperomia emarginella*, each 0.048 mm. long, while the smallest were those of *Miconia pycnoneura*, 0.010 mm. in length.

In considering the length of the guard cells in relation to the habit of the plant we found the following lengths:

8 taxa of herbaceous plants	average 0.031
2 taxa of woody epiphytes	average 0.030
24 taxa of trees or shrubs	average 0.028
5 taxa of woody climbers	average 0.027

The number of stomatal openings ranged from 18 per square mm. in *Guzmania berteroniana* to 230 per square mm. in *Isachne angustifolia*. Within the dicotyledons *Peperomia emarginella* had 22 stomata per square mm. while *Miconia pycnoneura* had 2230. While *Guzmania* had only 18 stomata per square mm., there were 96 stellate hair clusters in the same area.

*Vriesea sintenisii*, another bromeliad, was examined in several sections of the leaf. The upper portion of a mature leaf showed 11.4 stomatal apparatus per square mm. with 41.4 stellate hair-glands in the same area; the middle portion of the leaf had 28 stomata per mm.<sup>2</sup> and 19 stellate glands, while a basal portion above the water level showed 49.4 stomata per mm.<sup>2</sup> and 19 glands in the same area.

It has been suggested that metabolic activity of individual plants or leaves might be impaired by the presence of epiphyllous algae and leafy hepatics. The young leaves of most species within the forest are a bright green color when they first develop. In other species the young leaves were colored when young or expanding and developed a green color when near maturity. Young leaves of *Rajania* and *Ipomoea*, herbaceous vines, were bronze in color when young. Young leaves of the woody climbers *Gonocalyx* and *Hornemannia* were pink to red or orange-red in color. *Cleyera* and *Symplocos* also produced young leaves bronze in color, while *Calycogonium* had the young leaves reddish. The herbaceous *Peperomia hernandiifolia* had reddish young leaves. *Miconia pachyphylla* was unique in losing the green pigments and having the leaves turn a bright red or orange immediately before falling.

Upon reaching mature size, the leaves of most species in the Pico del Oeste elfin woodland acquired a covering of epiphyllous non-vascular plants. Spores, gemmae, gemmalings and sporelings, or fragments of liverworts are wind-borne and settle on the new leaves of most species. They appeared most quickly on species with depressed midrib or veins such as *Marcgravia*, *Ilex*, *Symplocos*, *Gonocalyx* or *Tabebuia*, and were rarely seen on the pubescent leaves of *Miconia foveolata* or the rugose leaves of *Miconia pycnoneura*. Dr. Margaret Fulford, in work to be reported later,

examined a collection of leaves from plants within the forest and in 94 collection numbers found approximately 680 specimens belong to 40 genera and more than 75 species. There appeared to be an average of eight species per sample with a maximum of 18 species. Preliminary data showed the following epiphyllous species distribution on representative leaves:

<i>Anthurium dominicense</i>	4	<i>Miconia pachyphylla</i>	5
<i>Ardisia luquillensis</i>	3	<i>Miconia pycnoneura</i>	8
<i>Calyptranthes krugii</i>	8	<i>Ocotea spathulata</i>	6
<i>Eugenia borinquensis</i>	2	<i>Peperomia emarginella</i>	1
<i>Gonocalyx portoricensis</i>	2	<i>Symplocos micrantha</i>	1
<i>Grammadenia sintenisii</i>	7	<i>Trichilia pallida</i>	6
<i>Ilex sintenisii</i>	12	<i>Wallenia yunquensis</i>	11
<i>Micropholis garciniaefolia</i>	8		

The number of epiphyllous taxa on any given leaf is not indicative of the leaf size or the percentage of the surface covered. The speed with which epiphyllae grew and covered the surface of the host was startling. Leaves of *Eugenia borinquensis* were completely and densely covered with liverworts in less than five months after leaf expansion. The amount of light reaching the photosynthetic area of the leaf is certainly reduced by the abundant epiphyllous growth. Epiphyllous growth occurred on leaves exposed at the summit of the canopy although the number of seemingly dead or desiccated plants was high. The leaves of the lower and inner branches of the forest components were more densely covered. Epiphyllae were less common on leaves of the truly herbaceous species.

#### LEAF DAMAGE

An additional factor in reducing the potential metabolic production of the plants in the elfin forest is evident in the amount of damage to the foliage of individual species. This has generally been attributed to wind. Damage done by animals as found in the Pico del Oeste forest has not been recorded.

The sheared effect and directional growth of woody plants along sea coasts have been attributed to wind and to salt spray. Beard and Gleason and Cook have suggested the same factors are important in the shaping of the mountain-top forests in the West Indies. The effects of wind were observed in the canopy of Pico del Oeste. Within a few feet of the roof of our observation tower a slender stem of *Eugenia borinquensis* had worn a circular opening in the canopy of surrounding species. Branches of *Tabebuia rigida* were worn smooth through the cambium to the xylem by friction against each other due to movement in the wind. The leaves of *Prestoea montana* were broken and lacerated when they exceeded the shelter of the lee forests. The soft leaves of *Psychotria berteriana* were severely lacerated on a few plants growing in open areas. The soft flush growth of *Hornemannia*, *Gonocalyx* and *Marcgravia* was broken and leaves torn when the leading branches were whipped about in gusting winds.

Microscope slides which were exposed to collect wind-blown particles also revealed crystals of salt. We failed to find any quantities of salt crystals on leaves or any indications of leaf damage due to salt spray from ocean storms. Apparently the large amounts of rain water or precipitation from the clouds washed the leaves free of salt.

The succulent young leaves were severely damaged by the populations of insects which existed on Pico del Oeste. In column 6 of TABLE 1 is recorded the percentage of leaves of each species that was affected by animal damage.

The program of collecting foliage material for drying and future chemical tests permitted an assessment of damage to leaves on representative plants. Among the monocotyledons, animal damage was relatively light and only plants of *Rajania cordata* and *Brachionidium parvum* appeared to be severely affected. Many dicotyledonous species, however, were eaten with great regularity. In one plant of *Clusia grisebachiana* selected for study 98% of all leaves had been partially eaten and the reduction in leaf surface was 24%. These figures were computed by an actual count of the leaves which had been eaten by insects, and the degree of surface loss computed by reconstructing the outline where possible, and measuring the area lost by planimeter. Eighty percent of all leaves on representative plants of *Haenianthus salicifolius*, *Wallenia yunquensis*, *Eugenia borinquensis* and *Miconia foveolata* were similarly eaten. *Miconia* showed a reduction in leaf surface of 35% and *Eugenia borinquensis* exhibited loss of 25%. The following table shows the plants most susceptible to insect damage.

	PERCENT DAMAGED	PERCENT REDUCTION IN SURFACE AREA	pH	PERCENT WATER
<i>Clusia grisebachiana</i>	98	24	3.9-4.3	66
<i>Haenianthus salicifolia</i>	86	19	5.1-5.2	62
<i>Wallenia yunquensis</i>	84	16	3.5-4.2	75
<i>Eugenia borinquensis</i>	81	25	4.8	30
<i>Miconia foveolata</i>	81	35	3.9-4.0	71
<i>Miconia pachyphylla</i>	79	21	3.7-4.3	60
<i>Grammadenia sintenisii</i>	77	—	4.1-4.5	84
<i>Hornemannia racemosa</i>	73	—	3.9-5.3	67
<i>Rajania cordata</i>	70	—	4.9	—
<i>Peperomia hernandiifolia</i>	70	—	4.6-5.1	—

The nature of the leaf damage varied. In most cases the insect began on the margin and ate for varying distances towards the midrib. In other cases the apex of the leaf was chosen as the point of initial attack. *Miconia pachyphylla* and *Miconia foveolata*, with the characteristic reticulate network of veins of the family, were characterized by holes in the leaves. No evidence was found of insect or animal attacks on the petioles or pulvini. Insect attacks seemed to be present at all months of the year. Damage to unexpanded primordia was rarely seen. Young leaves of a flush might be consumed completely as quickly as they began to expand in *Calypttranthes* and *Eugenia*. Other leaves were attacked only as the

lamina developed. The majority of the damaged leaves persisted on the plant following the insect attack. The leaves subsequently developed callous tissue or what appeared to be cork in many instances along the margin of laminar tissues that had been eaten.

Regrettably, we have been unable, up to this stage, to obtain scientific names or determinations for the insects seen or collected during this study. The following tabulation suggests that the food habits of the insects were often specific:

Gray caterpillar which stings: *Cleyera*, *Grammadenia*, *Miconia pycnoneura*.

Gray caterpillar with tufts of orange hairs and longer white hairs: *Ilex*, *Clusia*.

Slender green walking stick: *Eugenia*, *Marcgravia*.

Tan-colored stouter walking stick: *Miconia pycnoneura*.

Large spiny walking stick: *Ardisia*, *Calycogonium*, *Micropholis*, *Wallenia*.

A weevil: *Calycogonium*.

Spittle bugs: *Eugenia*.

Green grasshopper with white lines: *Tabebuia*.

Black grasshopper: *Tabebuia*.

Leaf hopper: *Cyathea*.

Leaf miners: *Hornemannia*.

A slug (*Gaeotis nigrolineata* Shuttleworth): *Lobelia*.

A snail (*Luquillia luquillensis* Shuttleworth): *Lobelia*.

Gall-producing insects: *Ocotea*.

No domatia were encountered in leaves of species within the elfin forest, although domatia were found in other species of plants in forests of lower elevations.

The nature of the attraction in the leaves of the component species to the insects cannot be determined. It was evident that the leaves varied in their texture, the amount and the color of the liquid within the tissues, their aromatic constituents and the pH of the cell contents. *Clusia* (Guttiferae), *Micropholis* (Sapotaceae), and *Lobelia* (Campanulaceae) possessed a latex, as is characteristic for the families involved. Ninety-eight percent of the leaves of *Clusia*, 33% of the leaves of *Micropholis* and 11% of the leaves of *Lobelia* were damaged by insects or snails. *Ipomoea repanda* also has cells containing a yellow material, although this did not flow when the leaf tissue was broken, and 61% of the leaves of this plant were damaged by insects. *Hedyosmum arborescens*, *Calycogonium squamulosum*, *Miconia foveolata*, and *Symplocos micrantha* could be classified as "bleeders," for the leaves, petioles or stems exuded a clear liquid when cut or broken. The percentage of leaves damaged by insects in these taxa were: *Hedyosmum*, 61%; *Calycogonium*, 21%; *Miconia foveolata*, 81%; and *Symplocos*, 14%. Aromatic principles were present in the leaves or bark of some species and can be described as follows: *Calycogonium* — cider odor; *Ilex* — odor of hay; *Mecranium* — sweet; *Miconia foveolata* — rank; *Miconia pachyphylla* — sweet; *Miconia pycnoneura* — sweet; *Symplocos* — rank and acidic; *Tabebuia* — medicinal; and *Wallenia* — odor of spinach. The nature of insect damage in these taxa is reported in TABLE 1, column 6.

In the preparation of several pounds of dried material of leaves or branches for shipping and subsequent chemical analysis, it was evident that the species of the elfin forest contained different amounts of liquid and solid materials. Large quantities of certain plants would produce only a few pounds of dry weight material while other species clearly had less liquid to evaporate. Standard weight samples of leaves were obtained and dried in an oven to obtain the percentage of water in the leaves of each species. For mature leaves the percentage of water ranged from 93% in *Psychotria guadalupensis* and *Begonia decandra* to 44% for *Calypttranthes krugii*. Only 1% of the leaves of *Psychotria guadalupensis* were damaged by insects, 26% of the leaves of *Begonia* and 41% of the leaves of *Calypttranthes*. In the list of 10 most severely damaged species previously given, the percentage of water in leaf tissue varied from 60% to 84% of the taxa for which we have data. Clearly some factor other than the amount of liquid in the plant tissue was responsible for the insect damage.

The abundance of liquid in some leaves led us to a simple measurement of the pH of the plant liquid which could be extracted (TABLE 1, column 7). Further details on these tests will be given in a later paper. For each species, leaves of a size normally eaten by insects were crushed between clean microscope slides and several drops of liquid were tested immediately with a Beckman pH meter. The acidity varied from 2.4 in *Begonia decandra* to 6.5 in *Justicia martinsoniana*. The values of the plant sap in the 10 most commonly eaten species ranged from 3.5 in *Wallenia yunquensis* to 5.3 in *Hornemannia racemosa* but averaged 4.4.

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Table 1

COLUMN 1—Total number of leaves per plant. COLUMN 2—Total photosynthetic area in cm.<sup>2</sup> COLUMN 3—average blade area in cm.<sup>2</sup> COLUMN 4—Ratio, blade length:width. COLUMN 5—Ratio, blade length:petiole length. COLUMN 6—Percent of leaves attacked by animals. COLUMN 7—pH of leaf sap. COLUMN 8—Percent of water in leaf tissue.

COLUMN NUMBER	1	2	3	4	5	6	7	8
GRAMINEAE								
<i>Arthrostylidium sarmentosum</i>	168	523	1.2	7.6:1	sessile	—	—	—
<i>Ichnanthus pallens</i>	12	97	8.1	3.5:1	sessile	0	—	—
<i>Isachne angustifolium</i>	18	144	8.0	10:1	sessile	0	—	—
CYPERACEAE								
<i>Carex polystachya</i>	27	2240	11.9	38:1	sessile	0	—	—
<i>Eleocharis Yunquensis</i>	54	609	—	terete	sessile	0	—	—
<i>Scleria secans</i>	14	3101	62.0	70:1	sessile	0	—	—
PALMAE								
<i>Prestoea montana</i>	10	289,460	28,946.0	—	—	0	5.1–6.2	—
ARACEAE								
<i>Anthurium dominicense</i>	10	918	91.8	6.8:1	1:1	0	5.0–5.8	—
BROMELIACEAE								
<i>Guzmania berteroniana</i>	20	4,392	225.0	—	sessile	0	4.0	—
<i>Vriesea sintenisii</i>	19	1,581	80.0	3.7:1	sessile	0	5.1	83
DIOSCOREACEAE								
<i>Rajania cordata</i>	20	370	18.0	2.5:1	1:1	70	4.9	—
ZINGIBERACEAE								
<i>Renealmia antillarum</i>	8	736	92.0	3.1:1	constr.	0	4.8–5.3	—

COLUMN NUMBER	1	2	3	4	5	6	7	8
ORCHIDACEAE								
<i>Brachionidium parvum</i>	4	7.5	1.8	2.1:1	2:1	25	—	—
<i>Dilomilis montana</i>	17	140	8.0	4.1:1	decur.	0	—	—
PIPERACEAE								
<i>Peperomia emarginella</i>	62	12	0.19	1:1	1:1	0	5.0-5.5	—
<i>Peperomia hernandiifolia</i>	10	146	14.6	1.7:1	1:1	70	4.6-5.6	—
CHLORANTHACEAE								
<i>Hedyosmum arborescens</i>	2,339	44,908	19.1	2.3:1	7.5:1	61	4.5-5.6	83
MORACEAE								
<i>Cecropia peltata</i>	6	7,497	1,249.5	1.1:1	1.6:1	0	5.1	—
URTICACEAE								
<i>Pilea krugii</i> (larger lf.)	16	137	8.5	2.8:1	10:1	12	5.1-6.0	—
<i>Pilea yunquensis</i> (larger lf.)	11	100	9.0	1.6:1	2.2:1	14	5.5-6.4	—
LAURACEAE								
<i>Ocotea spathulata</i>	433	10,452	24.1	1.7:1	27:1	25	4.8-5.1	59
MELIACEAE								
<i>Trichilia pallida</i>	10	1,618	16.1	2.6:1	22:1	16	5.2-5.6	—
AQUIFOLIACEAE								
<i>Ilex sintenisii</i>	8,684	15,631	1.7	1.4:1	5.3:1	10	5.1-5.3	63
CELASTRACEAE								
<i>Torrabasia cuneifolia</i>	229	1,762	7.7	2:1	18:1	7	4.7-5.0	63
OCHNACEAE								
<i>Sauvagesia erecta</i>	205	153.9	0.75	2.8:1	9:1	0	4.9-5.6	—

MARCRAVIACEAE								
<i>Marcgravia sintenisii</i>								
juvenile leaf	—	—	1.0	1.3:1	sessile	34	—	—
adult leaf	1,280	13,824	10.8	2.5:1	26:1	47	4.6-5.4	72
THEACEAE								
<i>Cleyera albopunctata</i>	678	7,661	11.2	2.0:1	14:1	20	3.8-4.2	56
GUTTIFERAE								
<i>Clusia grisebachiana</i>	243	1,956	8.0	1.5:1	32:1	98	3.9-4.3	66
BEGONIACEAE								
<i>Begonia decandra</i>	63	1,109	17.6	2.9:1	6.5:1	26	2.4-2.9	93
MYRTACEAE								
<i>Calyptranthes krugii</i>	4,539	18,609	4.0	1.2:1	15:1	41	4.0-5.1	44
<i>Eugenia borinquensis</i>	573	23,493	41.0	1.0:1	41:1	81	4.8	51
MELASTOMATACEAE								
<i>Calycogonium squamulosum</i>	1,345	14,660	10.9	2.3:1	6:1	21	3.3-3.7	92
<i>Mecranium amygdalinum</i>	519	8,615	16.6	2.0:1	6.8:1	42	3.2-3.8	77
<i>Miconia foveolata</i>	131	4,661	35.5	1.9:1	3.4:1	81	3.9-4.0	69
<i>Miconia pachyphylla</i>	296	6,089	20.5	2.6:1	4.4:1	79	3.7-4.3	60
<i>Miconia pycnoneura</i>	84	1,637	19.4	2.2:1	5.0:1	26	3.3-3.8	—
ERICACEAE								
<i>Gonocalyx portoricensis</i>	1,315	2,235	1.7	1.2:1	6.0:1	10	3.3-4.0	79
<i>Hornemannia racemosa</i>	1,315	2,235	22.2	1.7:1	21.0:1	73	3.9-5.3	55
MYRSINACEAE								
<i>Ardisia luquillensis</i>	1,857	17,458	9.4	2.2:1	11.0:1	50	4.3-4.4	68
<i>Grammadenia sintenisii</i>	579	7,411	12.8	2.4:1	12.0:1	73	4.1-4.5	84
<i>Wallenia yunquensis</i>	18	300	16.6	3.3:1	28.0:1	84	3.5-4.2	74

COLUMN NUMBER	1	2	3	4	5	6	7	8
SAPOTACEAE								
<i>Micropholis garciniaefolia</i>	10,487	96,480	9.1	1.6:1	8.0:1	33	4.1-4.8	52
SYMPLOCACEAE								
<i>Symplocos micrantha</i>	32	268	8.3	2.5:1	20.0:1	14	4.0-4.8	60
OLEACEAE								
<i>Haenianthus salicifolius</i>	1,294	17,339	13.4	2.7:1	8.0:1	86	5.1-5.2	62
CONVOLVULACEAE								
<i>Ipomoea repanda</i>	18	205	11.3	2.5:1	5.0:1	61	4.5-6.2	—
BIGNONIACEAE								
<i>Tabebuia rigida</i>	2,680	60,040	22.4	1.9:1	8.3:1	60	5.0-5.5	72
GESNERIACEAE								
<i>Alloplectus ambiguus</i>	16	168	10.5	2.2:1	9.5:1	43	4.6-5.5	—
<i>Gesneria sintenisii</i>	256	9,022	35.2	2.3:1	8.9:1	67	5.3-5.7	84
ACANTHACEAE								
<i>Justicia martinsoniana</i>	9	47	5.2	2.5:1	11.4:1	0	4.1-6.5	—
RUBIACEAE								
<i>Hillia parasitica</i>	48	564	11.7	2.7:1	5.6:1	29	4.7-4.9	83
<i>Psychotria berteriana</i>	305	18,093	59.3	2.0:1	4.5:1	62	5.0-5.7	85
<i>Psychotria guadalupensis</i>	213	410	1.9	2.0:1	1.4:1	1	4.9-5.0	93
CAMPANULACEAE								
<i>Lobelia portoricensis</i>	416	20,300	48.7	3.4:1	4.5:1	11	4.7-5.0	79
COMPOSITAE								
<i>Mikania pachyphylla</i>	46	274	5.9	1.4:1	4.5:1	10	5.1-6.0	—

Table 2

COLUMN 1—Leaf thickness in  $\mu$ . COLUMN 2—Upper hypodermis (present x, absent 0). COLUMN 3—Lower hypodermis. COLUMN 4—Ratio, upper epidermis:upper hypodermis. COLUMN 5—Upper cuticle. COLUMN 6—Lower cuticle. COLUMN 7—Crystals (ra = raphides, rh = rhombic, d = druses, f = furuncle. COLUMN 8—idioblasts or sclereids present. COLUMN 9—Multiple palisade layer. COLUMN 10—Ratio of palisade layer to spongy mesophyll. Isodiam. = isodiametric cells only.

COLUMN NUMBER	1	2	3	4	5	6	7	8	9	10
PIPERACEAE										
<i>Peperomia emarginella</i>	275	x	0	1:10	0	0	d,ra	0	0	1:4.7
<i>Peperomia hernandiifolia</i>	625	x	0	1:3.0	0	0	d	0	0	isodiam.
CHLORANTHACEAE										
<i>Hedyosmum arborescens</i>	311	x,2x	0	1:1.3	0	0	0	0	0	1:2
MORACEAE										
<i>Cecropia peltata</i>	91	0	0	—	0	0	d	0	0	1:0.39
URTICACEAE										
<i>Pilea krugii</i>	146	0	0	—	0	0	f	0	0	1:1
<i>Pilea yunquensis</i>	146	0	0	—	0	0	f	0	0	1:1
LAURACEAE										
<i>Ocotea spathulata</i>	475	2x	0	1:1.2	x	x	0	0	x	1:1.5
MELIACEAE										
<i>Trichilia pallida</i>	209	0	0	—	x	x	rh	0	0	1:2.3
AQUIFOLIACEAE										
<i>Ilex sintenisii</i>	421	0	0	—	x	x	d	0	x	1:1.8
CELASTRACEAE										
<i>Torrabasia cuneifolia</i>	458	0	0	—	x	x	d	0	x	1:4.5
OCHNACEAE										
<i>Sauvagesia erecta</i>	141	x	0	1:1.5	0	0	d	0	0	1:1

COLUMN NUMBER	1	2	3	4	5	6	7	8	9	10
MARCGRAVIACEAE										
<i>Marcgravia sintenisii</i>	512	0	0	—	x	0	ra	0	x	1:2.13
THEACEAE										
<i>Cleyera albopunctata</i>	512	0	0	—	x	x	0	x	x	1:1.4
GUTTIFERAE										
<i>Clusia grisebachiana</i>	787	4-5x	0	1:10.5	x	x	d	0	x	1:2.0
BEGONIACEAE										
<i>Begonia decandra</i>	311	x	x	1:4.7	0	0	0	0	0	1:3.0
MYRTACEAE										
<i>Calyptranthes krugii</i>	549	0	0	—	x	x	rh	x	x	1:5.5
<i>Eugenia borinquensis</i>	512	0	0	—	x	x	d	0	x	1:2.8
MELASTOMATACEAE										
<i>Calycogonium squamulosum</i>	292	2x	0	1:2	x	0	rh	0	x	1:2.4
<i>Mecranium amygdalinum</i>	180	x	0	1:1.3	0	0	d	0	x	1:0.4
<i>Miconia foveolata</i>	180	x	0	1:1	x	0	d	x	x	1:0.8
<i>Miconia pachyphylla</i>	258	x	0	1:2	x	0	d	0	x	1:1
<i>Miconia pycnoneura</i>	209	x	0	1:1	x	0	d	0	x	1:1.2
ERICACEAE										
<i>Gonocalyx portoricensis</i>	625	x	0	1:1	x	x	rh	0	0	1:3.2
<i>Hornemannia racemosa</i>	384	2x	0	1:1	x	0	rh	0	x	1:3.5
MYRSINACEAE										
<i>Ardisia luquillensis</i>	274	0	0	—	x	0	d	0	0	1:4.0
<i>Grammadenia sintenisii</i>	329	0	0	—	0	0	d	0	0	1:2.2

<i>Wallenia yunquensis</i>	384	0	0	—	x	x	rh	0	x	1:1.5
SAPOTACEAE										
<i>Micropholis garciniaefolia</i>	512	x	0	1:1	x	x	0	0	x	1:1.6
SYMPLOCACEAE										
<i>Symplocos micrantha</i>	293	0	0	—	x	x	d	0	x	1:1.7
OLEACEAE										
<i>Haenianthus salicifolius</i>	457	0	0	—	x	0	0	x	x	1:1.6
<i>Ipomoea repanda</i>	329	0	0	—						
CONVOLVULACEAE										
					x	x	d	0	0	1:3.8
BIGNONIACEAE										
<i>Tabebuia rigida</i>	625	x	0	1:1.2	x	x	0	0	x	1:2.56
GESNERIACEAE										
<i>Alloplectus ambiguus</i>	256	0	0	—	0	0	0	0	0	1:2.5
<i>Gesneria sintenisii</i>	450	x	0	1:3	x	0	0	0	0	1:2.5
ACANTHACEAE										
<i>Justicia martinsoniana</i>	257	0	0	—	0	0	f	0	0	1:3.5
RUBIACEAE										
<i>Hillia parasitica</i>	403	x	x	1:2.7	x	x	ra	0	0	1:2.87
<i>Psychotria berteriana</i>	146	0	0	—	x	0	ra	0	0	1:0.7
<i>Psychotria guadalupensis</i>	823	x	0	1:15.2	x	x	ra	0	0	1:2.5
CAMPANULACEAE										
<i>Lobelia portoricensis</i>	147	0	0	—	x	0	0	0	0	isodiam.
COMPOSITAE										
<i>Mikania pachyphylla</i>	300	0	0	—	x	0	0	0	0	isodiam.

Table 3

COLUMN 1—Habit of plant: H = Herb; S = Shrub; T = Tree; WC = Woody climber; HC = Herbaceous climber; E = Epiphyte. COLUMN 2—Position of inflorescence: T = Terminal; A = Alternate; C = Cauliflorous. COLUMN 3—Type of growth or branching: M = Monopodial; S = Sympodial; A = Alternate; D = Dichotomous. COLUMN 4—Branches abort or show die-back. COLUMN 5—Type of leaf production: C = appearing continuously on plant; numbers refer to leaves or pairs of leaves produced in a flush. COLUMN 6—Number of leaves present. Hyphenated numbers refer to clear examples of number of leaves and number of flushes represented. COLUMN 7—Length of guard cells in mm. COLUMN 8—Number of stomata per sq. mm. COLUMN 9—Type of stomatal apparatus.

COLUMN NUMBER	1	2	3	4	5	6	7	8	9
PIPERACEAE									
<i>Peperomia emarginella</i>	H	T	M	—	C	—	.046	22	Anomocytic
<i>Peperomia hernandiifolia</i>	H	T	M	—	C	7	.032	65	Anisocytic
CHLORANTHACEAE									
<i>Hedyosmum arborescens</i>	S	T	S	—	3 pr	—	.046	75	Anomocytic
MORACEAE									
<i>Cecropia peltata</i>	T	A	A	—	C	—	.018	500	Anomocytic
URTICACEAE									
<i>Pilea krugii</i>	H	A	M	—	C	—	.023	65	Anisocytic
<i>Pilea yunquensis</i>	H	A	M	—	C	—	.023	110	Anomocytic
LAURACEAE									
<i>Ocotea spathulata</i>	T	A	S	—	1-3(7)	14-ss	.032	306	Paracytic
MELIACEAE									
<i>Trichilia pallida</i>	S	A-C	M	—	1	6-	.032	205	Anomocytic
AQUIFOLIACEAE									
<i>Ilex sintenisii</i>	S	A	A	DB	3-4	20-7	.023	140	Anomocytic
CELASTRACEAE									
<i>Torrabasia cuneifolia</i>	S	A	S	DB	C	20-7	.032	130	Anomocytic
OCHNACEAE									
<i>Sauvagesia erecta</i>	H	A	A	—	C	31-	.032	187	Paracytic
MARCRAVIACEAE									
<i>Marcgravia sintenisii</i>	C	T	M	—	C	40-	.028	90	Anomocytic
THEACEAE									
<i>Cleyera albopunctata</i>	T	A	A	DB	C	3-	.037	280	Anomocytic
GUTTIFERAE									
<i>Clusia grisebachiana</i>	T	T	D	—	2 pr	4-2	.036	177	Paracytic
BEGONIACEAE									
<i>Begonia decandra</i>	H	T	A	—	C	—	.035	270	Paracytic
MYRTACEAE									
<i>Calyptranthes krugii</i>	S	A	D	—	1-2 pr	—	.030	310	Paracytic
<i>Eugenia borinquensis</i>	T	A,C	D	DB	1-3 pr	15-20	.023	884	Anisocytic
MELASTOMATACEAE									
<i>Calycogonium squamulosum</i>	S	A	D	—	C	—	.016	550	Anisocytic
<i>Mecranium amygdalinum</i>	S	A,C	A	—	—	—	.018	680	Anomocytic
<i>Miconia foveolata</i>	S	T	D	—	—	6-	.016	1180	Anomocytic
<i>Miconia pachyphylla</i>	S	T	D	—	3-5 pr	5-	.035	130	Anomocytic
<i>Miconia pycnoneura</i>	S	T	D	—	C	5-	.010	2230	Anomocytic
ERICACEAE									
<i>Gonocalyx portoricensis</i>	C	A,C	A	—	3-4	20-4	.020	411	Paracytic
<i>Hornemannia racemosa</i>	C	A	A	DB	C	9-	.021	340	Paracytic
MYRSINACEAE									
<i>Ardisia luquillensis</i>	T	T	S	DB	5	—	.025	230	Anisocytic
<i>Grammadenia sintenisii</i>	S	A	S	—	C	—	.025	159	Anisocytic
<i>Wallenia yunquensis</i>	S	A	S	—	—	5-	.030	177	Paracytic

COLUMN NUMBER	1	2	3	4	5	6	7	8	9
SAPOTACEAE									
<i>Micropholis garciniaefolia</i>	T	A	A	DB	2-6	20-4	.027	230	Anomocytic
SYMPLOCACEAE									
<i>Symplocos micrantha</i>	S	A	A	—	2-6	—	.030	230	Paracytic
OLEACEAE									
<i>Haenianthus salicifolius</i>	T	T	D,S	—	C	—	.025	327	Anomocytic
CONVOLVULACEAE									
<i>Ipomoea repanda</i>	WC	A	A,T	DB	C	9-	.032	110	Paracytic
BIGNONIACEAE									
<i>Tabebuia rigida</i>	T	T	D	DB	1-2 pr	10-4	.023	230	Anomocytic
GESNERIACEAE									
<i>Alloplectus ambiguus</i>	H	A	M	DB	C	22-	.032	56	Anisocytic
<i>Gesneria sintenisii</i>	S	A	M	DB	C	20-	.035	168	Anisocytic
ACANTHACEAE									
<i>Justicia martinsoniana</i>	H	T	D	—	—	—	.025	170	Paracytic
RUBIACEAE									
<i>Hillia parasitica</i>	S,E	T	D	—	—	—	.037	100	Paracytic
<i>Psychotria berteriana</i>	S	T	D	—	2 pr	3-	.029	210	Paracytic
<i>Psychotria guadalupensis</i>	S,E	T	½D	—	C	8-	.025	110	Paracytic
CAMPANULACEAE									
<i>Lobelia portoricensis</i>	S,H	T	A	DB	—	37-	.040	190	Anomocytic
COMPOSITAE									
<i>Mikania pachyphylla</i>	C	A,T	M	—	—	—	.035	196	Anomocytic

Table 4

TAXON	STOMATAL SIZE IN MM.	STOMATA NUMBER MM <sup>2</sup>	TYPE OF STOMATAL APPARATUS
GRAMINEAE			
<i>Arthrostylidium sarmentosum</i>	0.027	205	Gramineous
<i>Ichnanthus pallens</i>	0.043	140	Gramineous
<i>Isachne angustifolium</i>	0.023	230	Gramineous
CYPERACEAE			
<i>Carex polystachya</i>	0.041	102	Gramineous
<i>Eleocharis yunquensis</i>	0.048	120	Gramineous
<i>Scleria secans</i>	0.030	110	Gramineous
PALMAE			
<i>Prestoea montana</i>	0.025	140	Paracytic
ARACEAE			
<i>Anthurium dominicense</i>	0.046	56	Paracytic
BROMELIACEAE			
<i>Guzmania berteroniana</i>	0.044	18	Didymocytic
<i>Vriesea sintenisii</i>	0.039	28	Didymocytic
DIOSCOREACEAE			
<i>Rajania cordata</i>	0.035	120	Anomocytic
ZINGIBERACEAE			
<i>Renealmia antillarum</i>	0.027	140	Paracytic
ORCHIDACEAE			
<i>Brachionidium parvum</i>	0.039	37.5	Didymocytic
<i>Dilomilis montana</i>	0.032	120	Anomocytic

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## EXPLANATION OF PLATES

## PLATE I

a. Terminal bud of an adult branch of *Marcgravia sintenisii*. b. Stem of *Hillia parasitica* showing the flattened stipular sheath. c. Stem apex of *Ilex sintenisii* showing the rosette of small leaves and cataphylls. d. Shoot apex of *Gesneria sintenisii* showing the individual leaf primordia; each primordium is encased in a resinous covering. e. Section through the apex of *Hedyosmum arborescens* revealing the stem apex and young leaves encased in the sheathing bases of petioles. f. *Clusia grisebachiana*, in which the leaves of the apical pair are tightly appressed and enclose and protect the terminal bud. g. Three views of the stem apex and terminal leaf pair of *Calyptrocalyx krugii*, left figure shows the mature leaves; central figure shows the plicate stipule pair separated at the base; right figure shows the plicate stipule pair separated at the apex.

## PLATE II

a. Cross section of a leaf of *Haenianthus salicifolius* showing the multiple layers of palisade parenchyma and two branched idioblasts. b. View of the upper epidermis of *Pilea krugii* showing two furuncles. c. Cross section of a leaf of *Peperomia hernandiifolia* showing the irregular epidermis, the multiple hypodermis, a layer of parenchyma containing druses and the undifferentiated mesophyll containing chloroplasts. d. Cross section of a leaf of *Mikania pachyphylla* showing the undifferentiated mesophyll.

## PLATE III

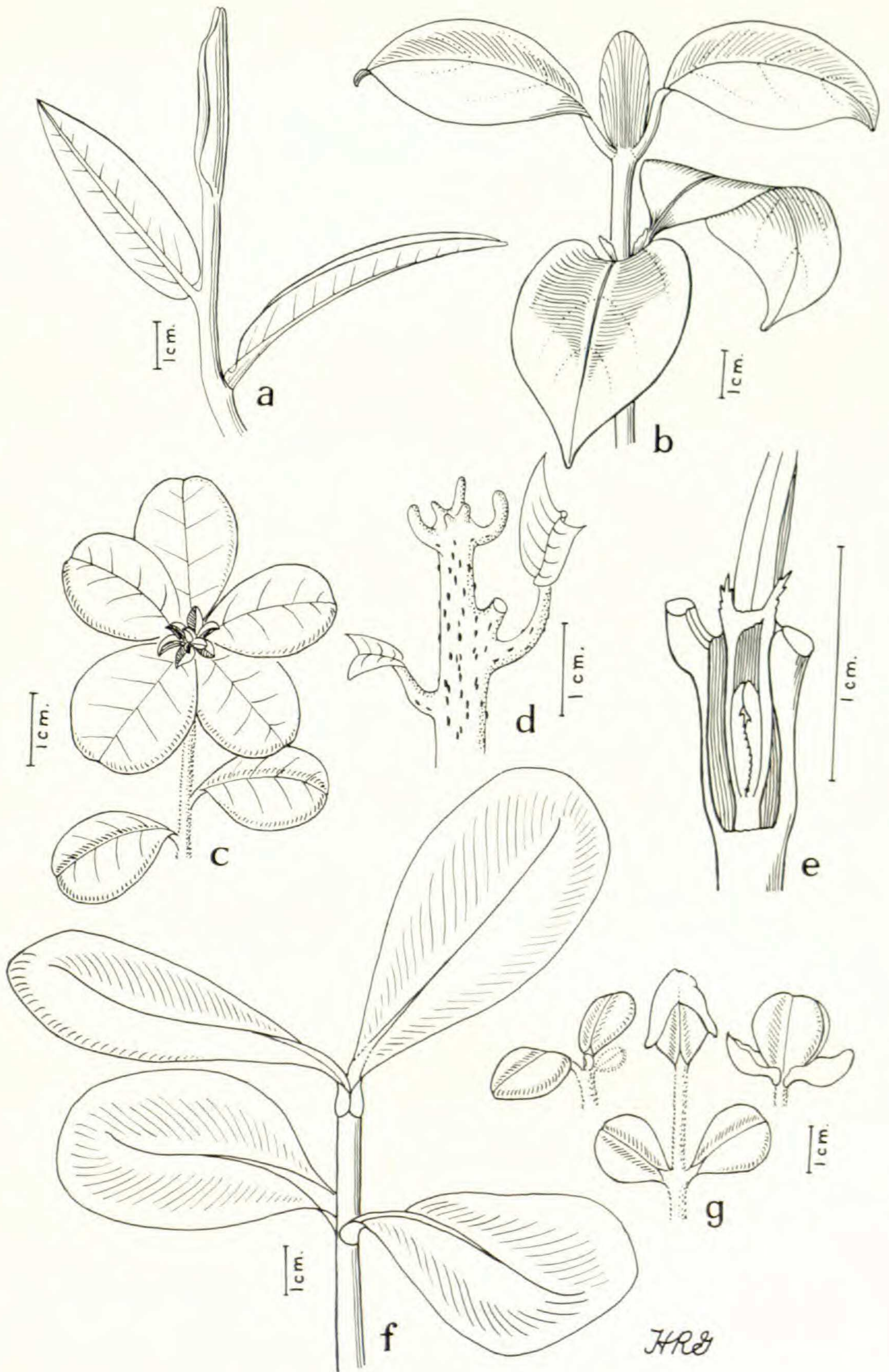
Epidermal cells and stomatal apparatus of: a, *Miconia pachyphylla*; b, *Brachionidium parvum*; c, *Alloplectus ambiguus*; d, *Renealmia antillarum*.

## PLATE IV

Epidermal cells and stomatal apparatus of: a, *Anthurium dominicense*; b, *Hillia parasitica*; c, *Torrabasia cuneifolia*; d, *Scleria secans*; e, *Haenianthus salicifolius* var. *obovatus*; f, *Gonocalyx portoricensis*.

## PLATE V

a. Lower epidermal surface of *Pilea krugii* showing the cluster of small stomata over a vascular bundle, a multicellular gland, and two of the larger stomatal apparatus. b. The lower epidermal surface of a leaf of *Grammadenia sintenisii* showing the stomatal apparatus grouped in clusters of three.

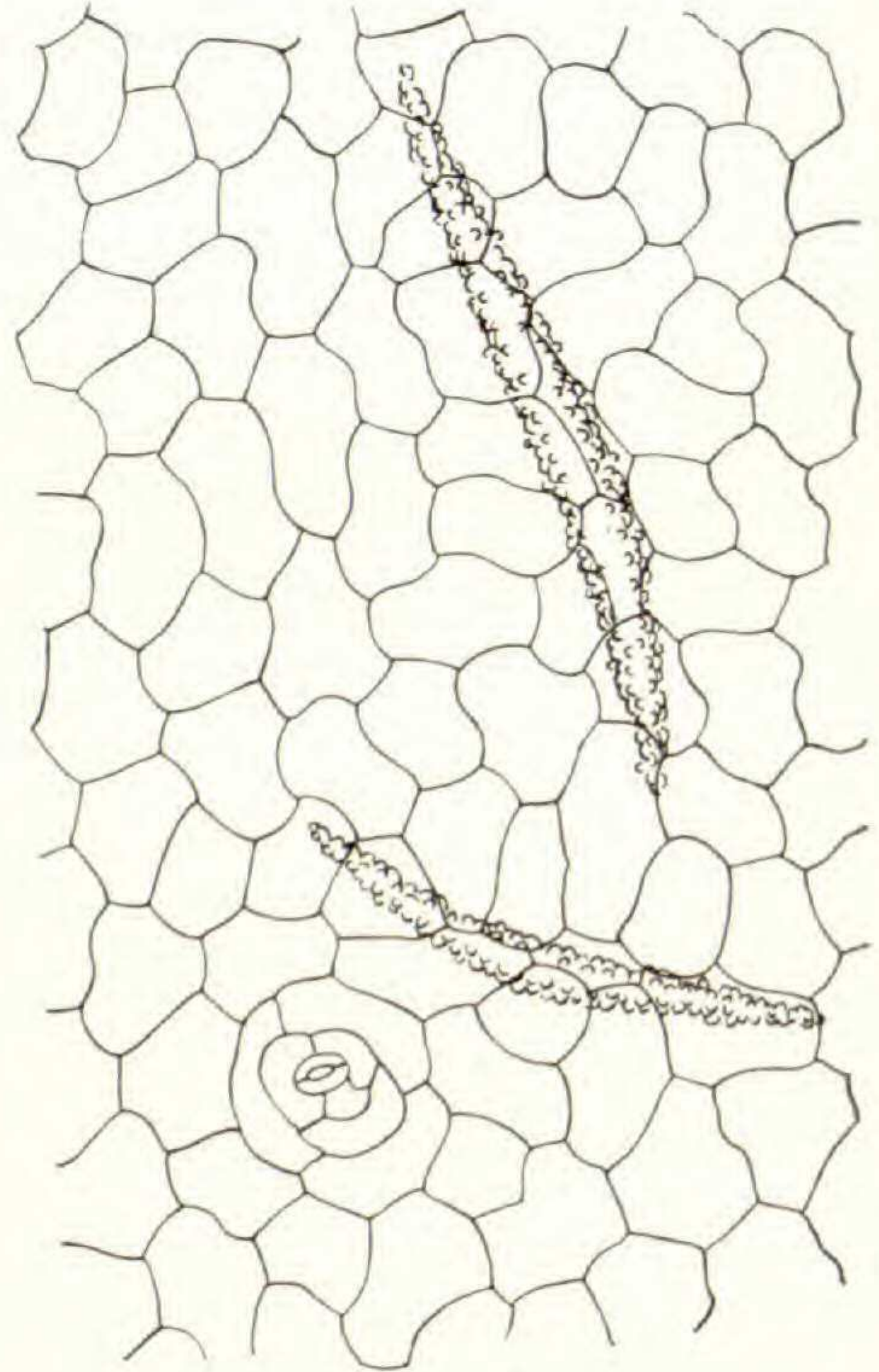


HRB

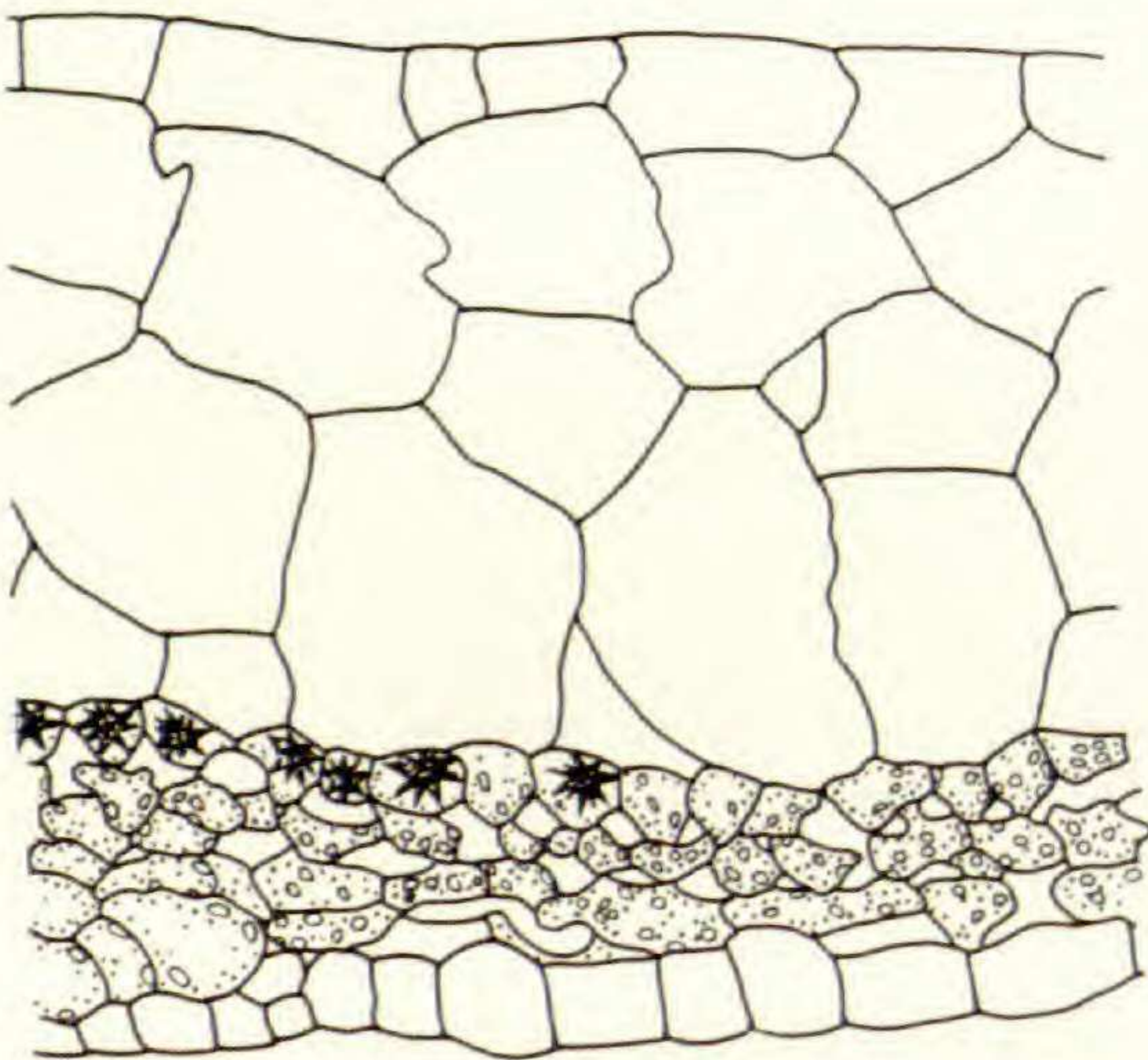
HOWARD, ELFIN FOREST, 8



a

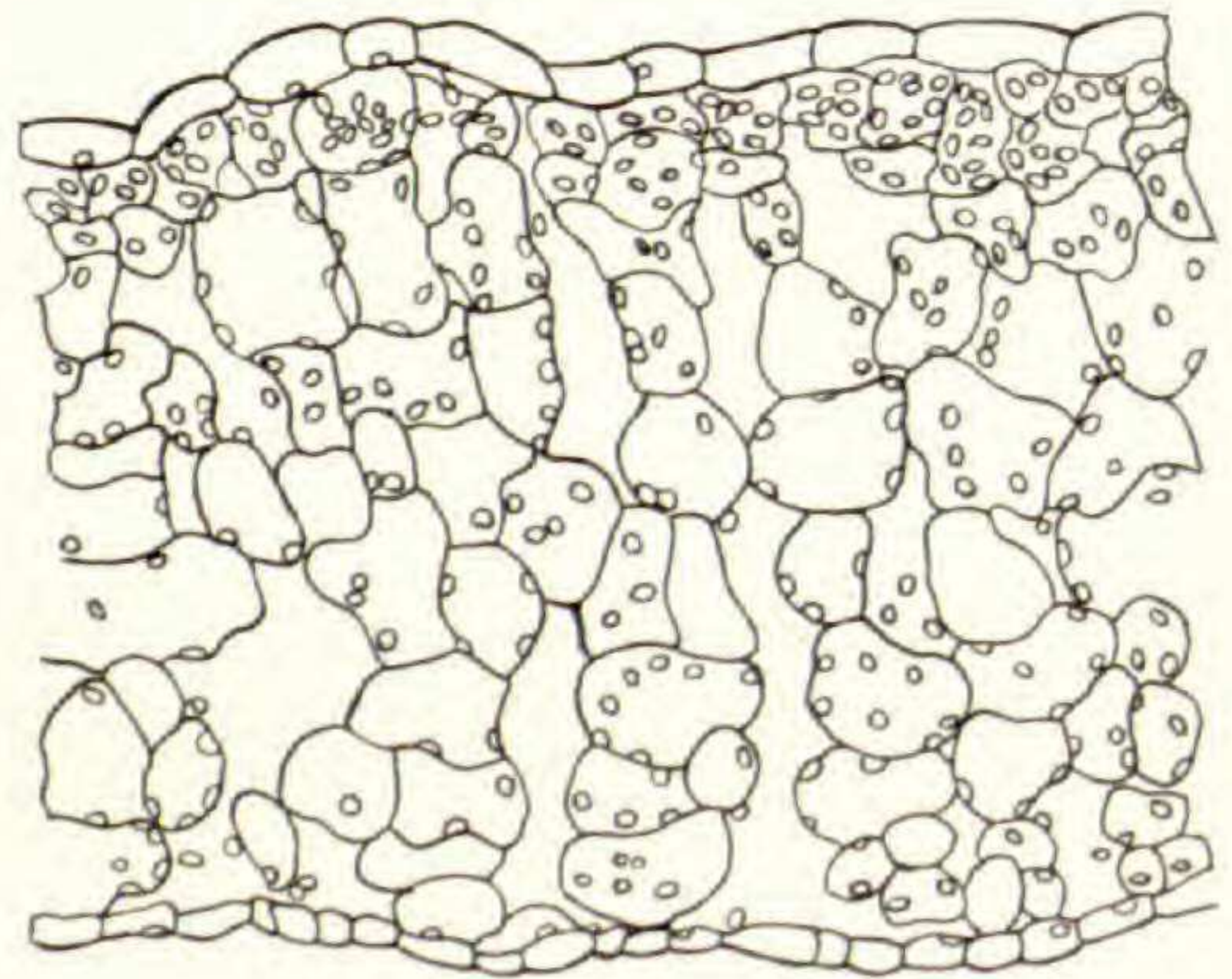


b



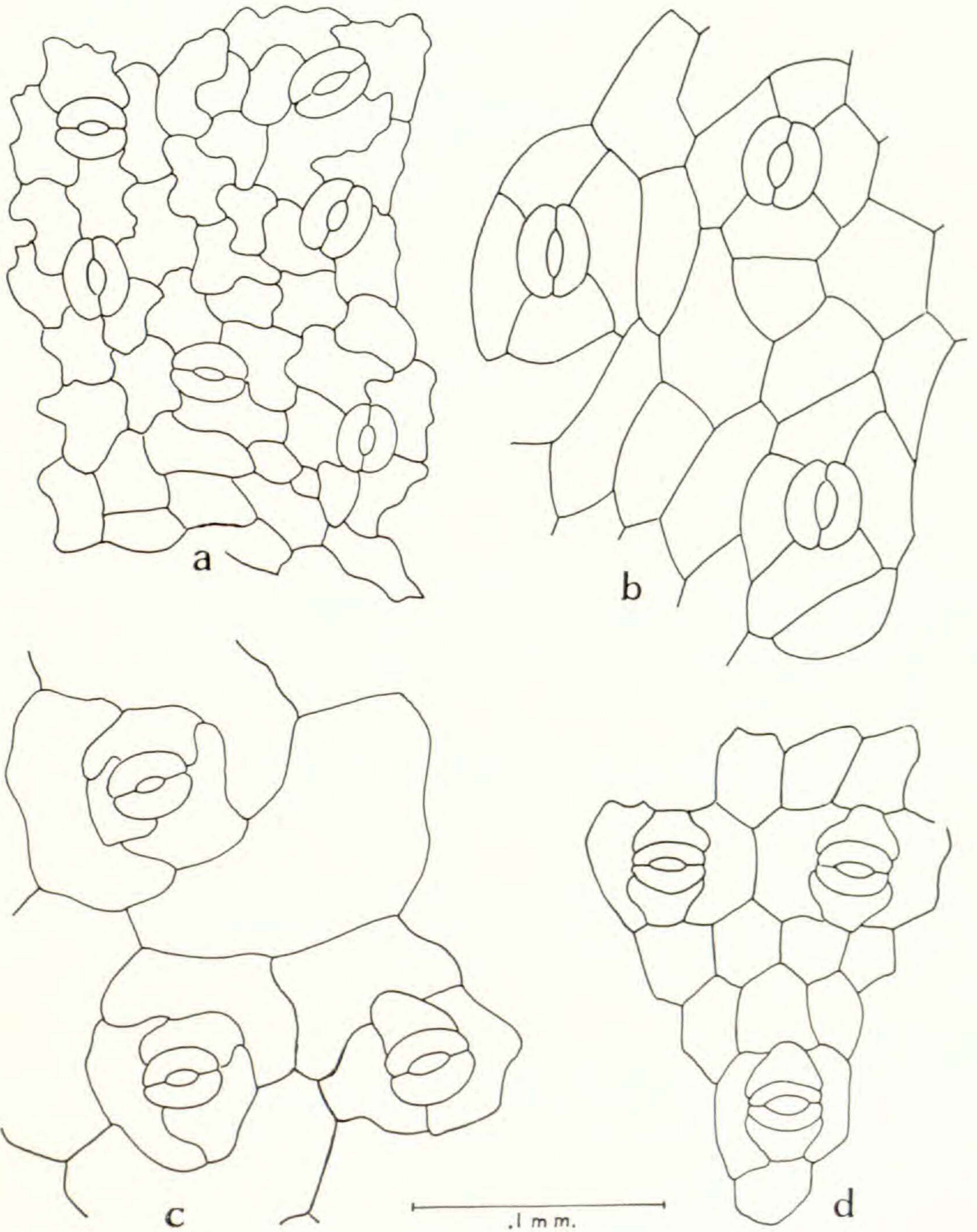
c

.1 mm.

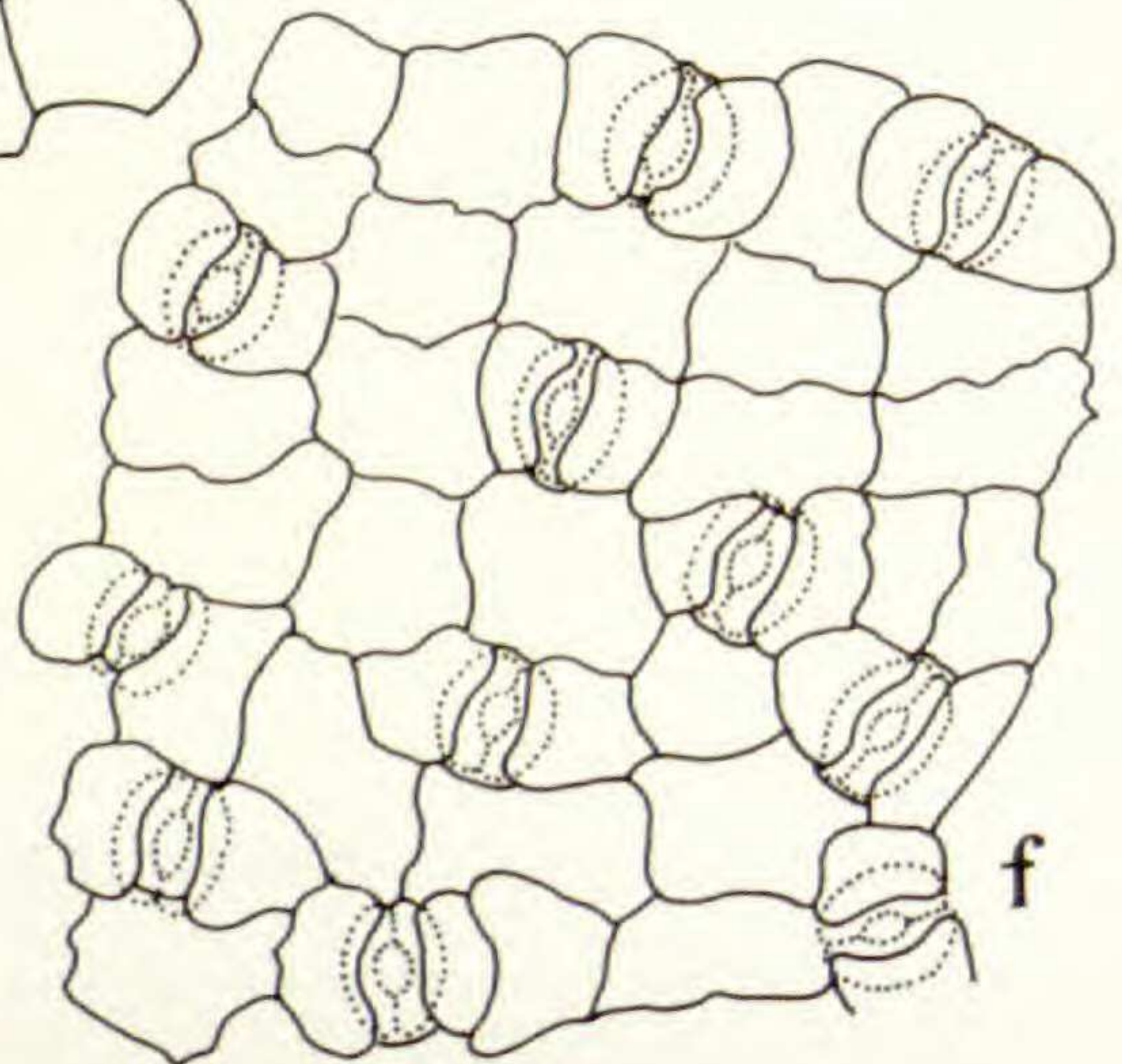
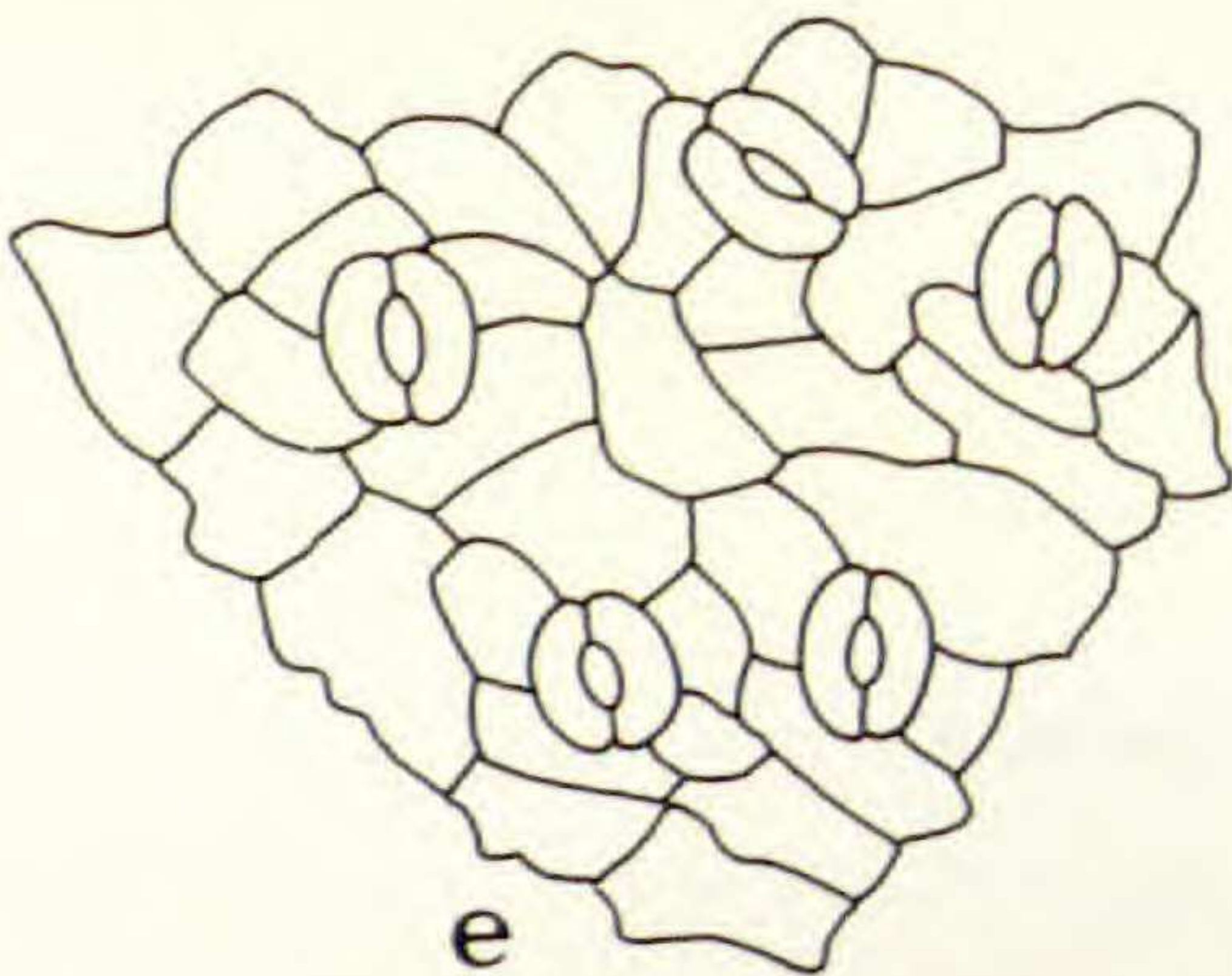
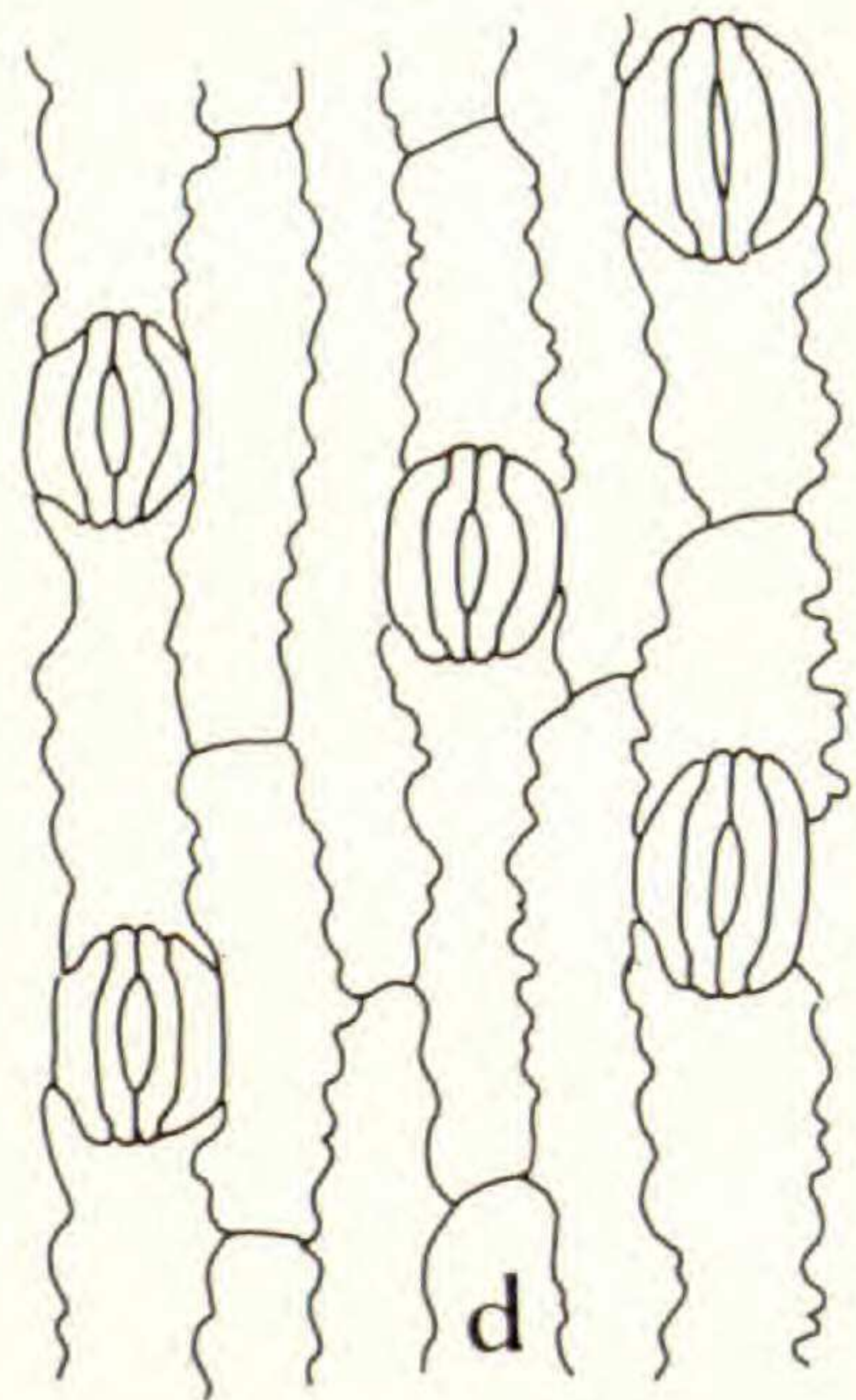
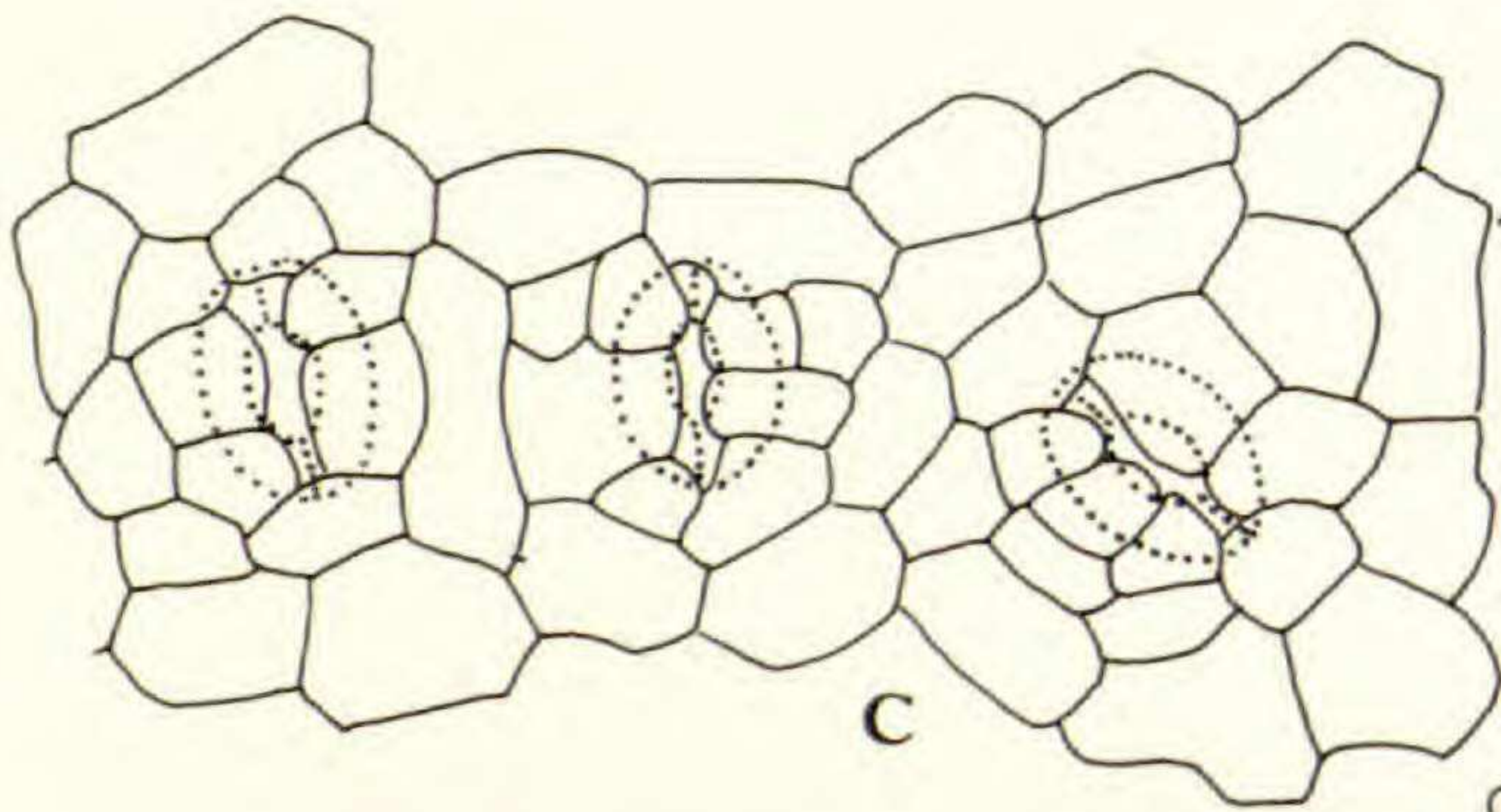
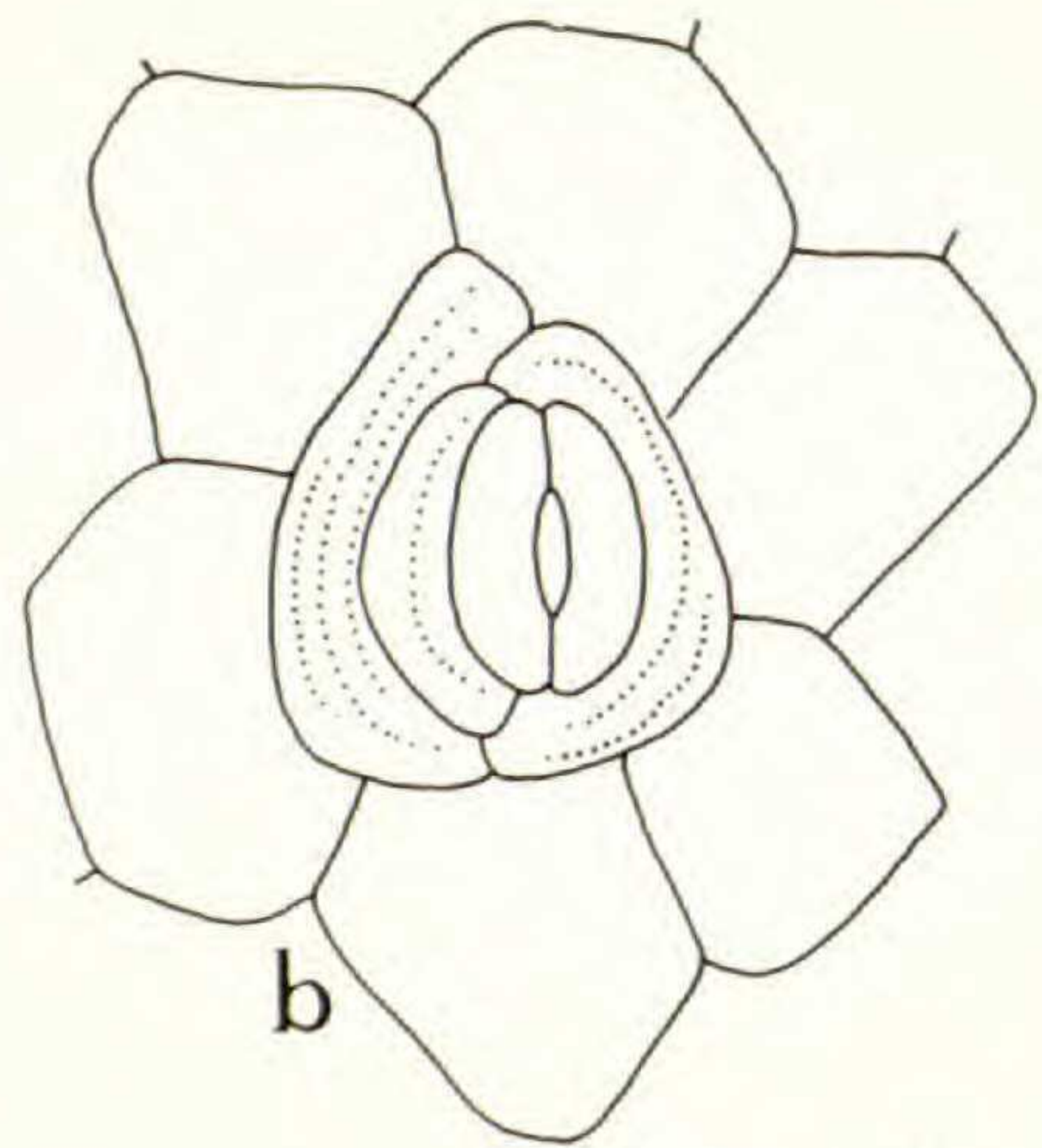
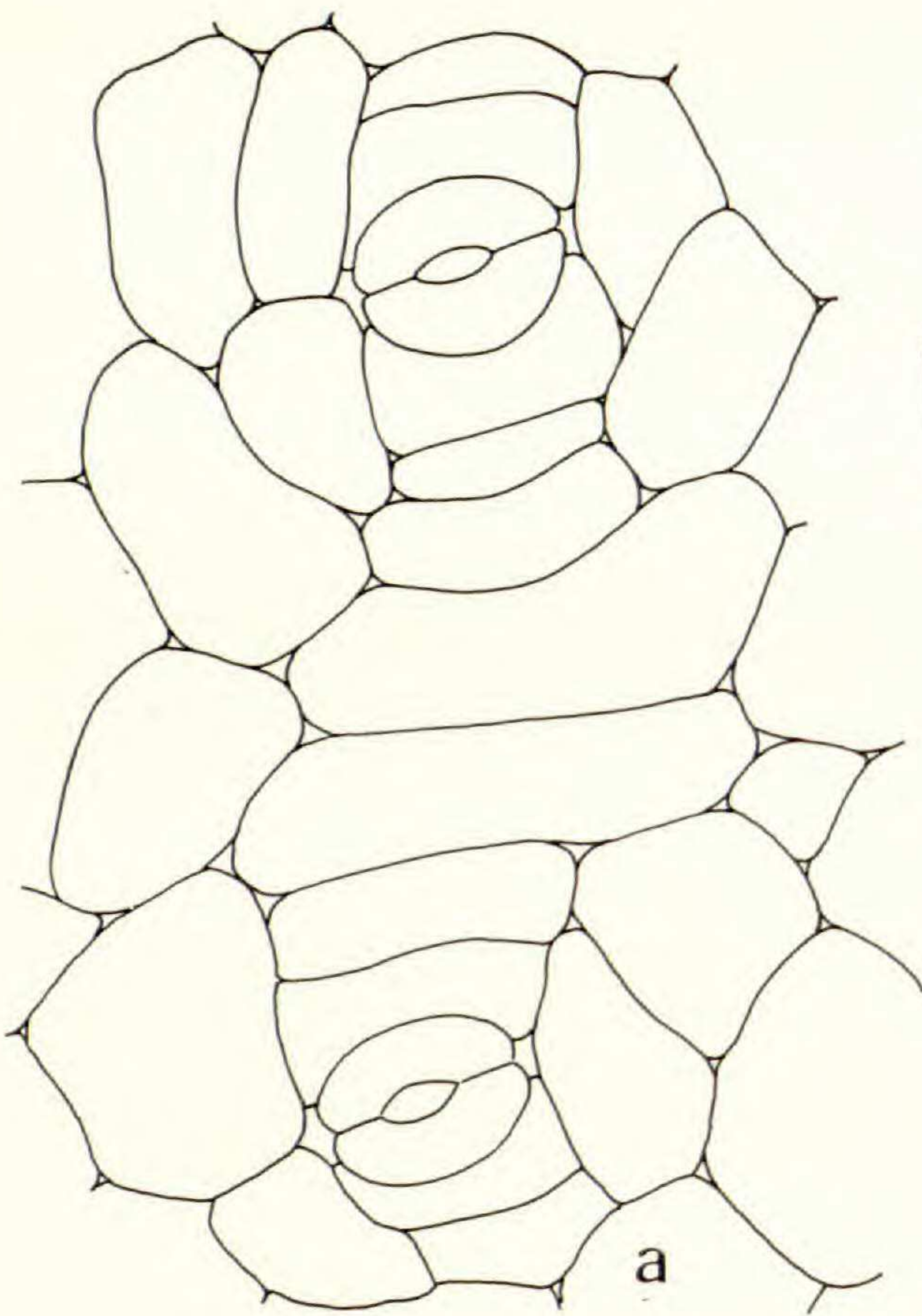


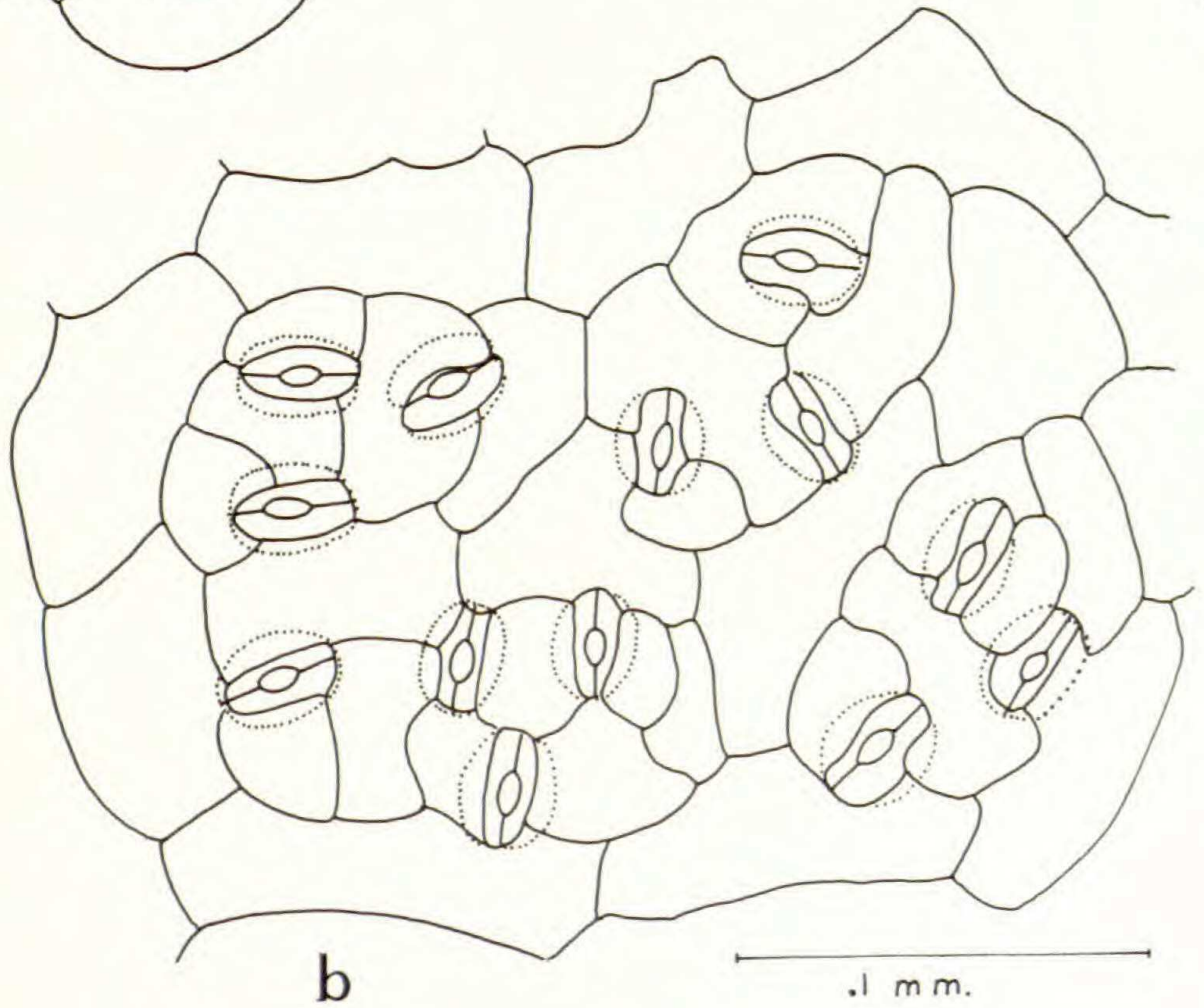
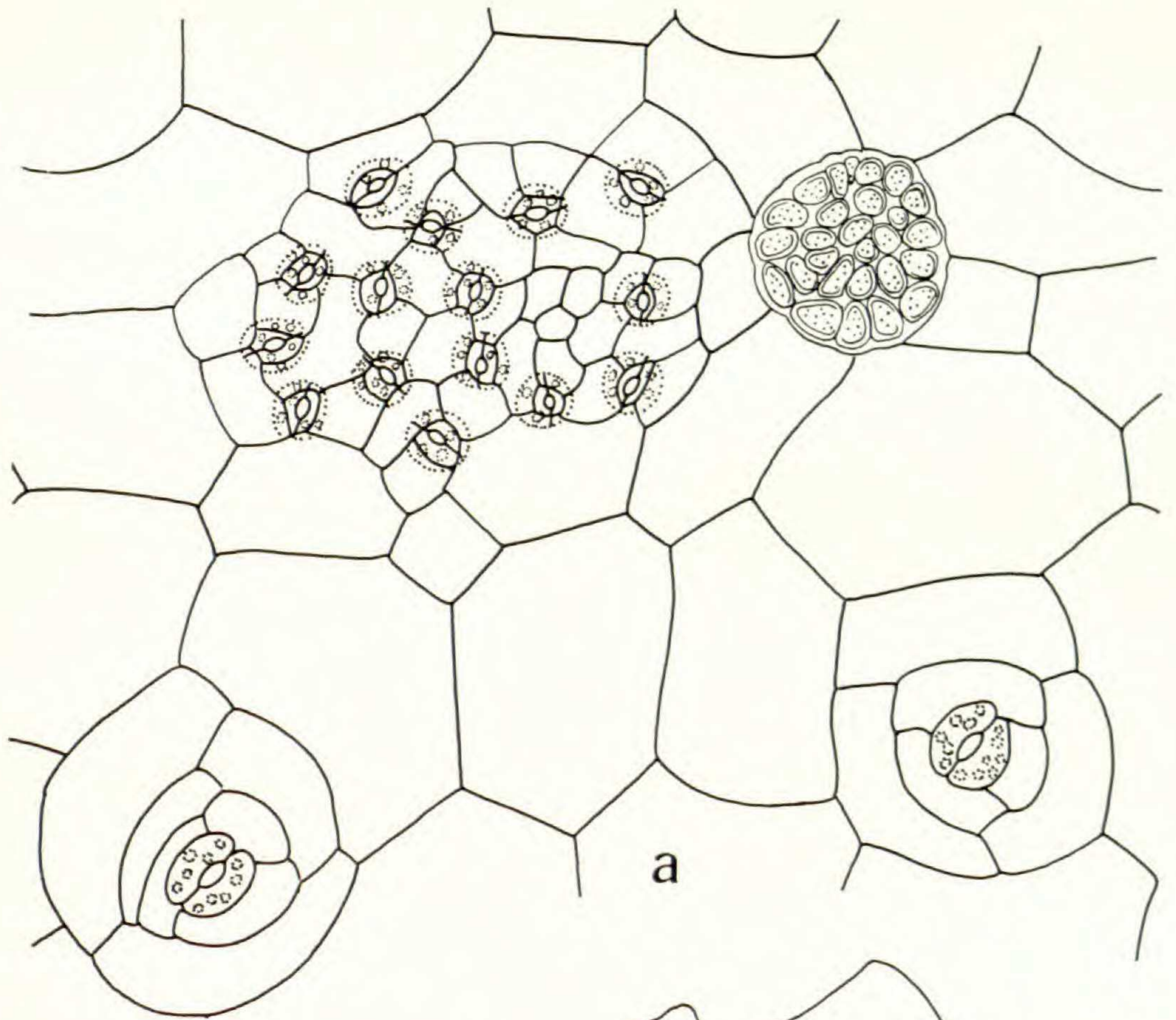
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LECTOTYPIFICATION OF CACALIA L.  
(COMPOSITAE-SENECIONEAE)<sup>1</sup>

BERYL S. VUILLEUMIER AND C. E. WOOD, JR.

THE INTERNATIONAL CODE of Botanical Nomenclature (1966) provides, by means of nomenclatural types, stability in the application of names at, or below, the rank of family. The use of a name is determined by the nomenclatural type of that name, and changes may result when, or if, the choice of a type is shown to be incorrect. To avoid disadvantageous changes in the application of names provision is also made in the Code to preserve current usage and to avoid the confusion which could result from varying opinions concerning the choice of a lectotype. The senecionid genus *Cacalia*, as circumscribed by Linnaeus (1753, 1754) was quite heterogeneous, and the process of choosing a lectotype has been both complicated and subject to individual interpretation. Three different species have been proposed as lectotype, and even now there are conflicting opinions (Cuatrecasas, 1960, and Pippen, 1968, *vs.* Pojarkova, 1961, and Vuilleumier, 1969). It seems expedient to review the typification of this genus once more. *Cacalia* as typified here (by *C. hastata* L., a choice made by Kitamura, 1942) provides an example in which the choice of a lectotype in accordance with the guides outlined in the Code also complies with the recommendation (7B) that a lectotype be so chosen as to preserve current usage.

In the first edition of *Species Plantarum* (2: 834–836. 1753), Linnaeus described and named ten species of *Cacalia* which he divided into two groups: "Frutescentes," consisting of four shrubby species, and "Herbaceae," with six herbaceous species. In 1754, Miller (*Gard. Dict. Abr. ed. 4. 2: ord. alph.*) split *Cacalia*, placing the four shrubby species in *Kleinia* Mill. *Cacalia* was thus restricted to the herbaceous species, and it is from the six original species of this group that all choices of lectotype have been made. To our knowledge, no one has suggested that *Cacalia* be typified by one of the species removed to *Kleinia*.

There has been, however, considerable disagreement as to which of the six herbaceous species should be designated as lectotype. Rydberg (1924) concluded that *Cacalia alpina* should be the type species; Cuatrecasas (1955, 1960) and Pippen (1968) have concurred in this choice.

<sup>1</sup> One of an informal series of peripheral papers arising from research toward a *Generic Flora of the Southeastern United States* being carried on through the generous help of the National Science Foundation (Grant GB-6459X, C. E. Wood, Jr., principal investigator).

We acknowledge with thanks the assistance of Dr. Bernice G. Schubert and Dr. Elizabeth Shaw and we are indebted to Andrey I. Baranov for his translation of a portion of A. Pojarkova's treatment of *Cacalia* in Flora URSS.

Hitchcock and Green (1927) chose another type, *C. atriplicifolia*, which Pojarkova (1960) also adopted. Kitamura (1942), however, made a third choice, *C. hastata*, and Pojarkova (1961), changing her opinion, agreed with him. Quite independently, Shinnars (1950) came to the conclusion that either *C. suaveolens* or *C. hastata* should be the lectotype species. After a careful review of the arguments and of the nomenclatural and taxonomic history of *Cacalia* in conjunction with the application of the Rules and Recommendations of the Code, we are convinced that *C. hastata* should be the lectotype species.

Since the nomenclature of species of vascular plants begins in 1753 and that of genera in 1754, in most instances the application of a name prior to 1753 should be given little weight relative to a post-1753 application, especially since Linnaeus not infrequently reapplied older names in a completely different sense. However, one of the principal arguments advanced, first by Rydberg, and then by Cuatrecasas and Pippen for the selection of *Cacalia alpina* as the type species of *Cacalia* is an historic one. Rydberg wrote (*loc. cit.*, p. 370), "Of the species of the second [herbaceous] group only the last two, *Cacalia atriplicifolia* and *C. alpina*, had been known as *Cacalia* before Linnaeus' time.<sup>2</sup> The name *Cacalia*, applied to the last one, dates back to Vaillant and L'Obel. *C. alpina* L. or *Adenostylis alpinus* is therefore the historical type of *Cacalia*." Cuatrecasas (1960, p. 182) reiterated, "There is no doubt that the name *Cacalia* was first applied to *C. alpina* and that Linné had this species in mind when he established the genus in his *Genera Plantarum*. Therefore, *Cacalia alpina* is the type of *Cacalia*." Pippen added (1968, p. 377), "It seems clear that *C. alpina* L. is the most logical lectotype of *Cacalia*. This species, named *C. alpina* by Linnaeus (1753), embodied the Linnaean and pre-Linnaean concept of *Cacalia* in that essentially all of the species of *Cacalia* described by pre-Linnaean botanists (L'Obel, 1581; Clusius, 1601; Bauhin, 1623; Morison, 1699; Tournefort, 1700) actually represented the same species."

The adoption of this historical argument would restrict the name *Cacalia* to a genus consisting of four or five species of Europe which has been known since 1816 as *Adenostyles* Cassini. Contrary to all three authors, however, the use of arguments concerning the application of names before the starting point for botanical nomenclature can result only in further confusion, as is shown below.

In the first edition of *Genera Plantarum* (1737, p. 252), *Cacalia* in the sense of Tournefort (that is, *C. alpina* L.) is found in the synonymy of *Tussilago*: "TUSSILAGO\*. *Tournef.* 276. *Vaill.* A. G. 1720. f. 46. *Cacalia*

<sup>2</sup>In the next paragraph Rydberg added, ". . . only Linnaeus himself had used *Cacalia* for *C. suaveolens* in his *Hortus Upsaliensis*." Rydberg probably was misled by Linnaeus's reference to *Hortus Upsaliensis* immediately following the diagnostic phrase name (specific name) of *Cacalia suaveolens* in *Species Plantarum* (1753, p. 835). In *Hortus Upsaliensis* (1748, p. 254), Linnaeus treated this as a species of *Kleinia* ("Kleinia caule herbaceo," etc.); the diagnosis is the same in *Species Plantarum*, except that *Cacalia* has been substituted for *Kleinia*. We have not found any mention of *Cacalia* in *Hortus Upsaliensis*.



*Tournef.* 258. *Petasites Tournef.* 258. *Vaill. A. G.* 1719." Following the description the observation is added: "*Cacalia T. caule ramoso est, & corollulis hermaphroditis quadrifidis, sine radio ligulato.*" On the same page is found *Kleinia*: "KLEINIA. *Cacalanthemum Dill. elth.* 54. 55. An *Tithymaloides*? *Klein. monagr.*" The corolla is described as with the limb "quinquefido, erecto," and the stigmas as "duo, oblonga, revoluta." In the second edition (1742, p. 401), the synonymy of *Tussilago* is amplified by the addition of "*Vaill. A. G.* 1719." to the reference to *Cacalia*, and to that of *Kleinia* (p. 394) is added "*Porophyllum Vaill. A. G.* 1719. t. 20. f. 39." which Linnaeus had maintained as distinct in the *Hortus Cliffortianus* (1738, p. 494). Neither description was changed in any way in this edition. The synonymy and descriptions of *Tussilago* and *Kleinia* in the editions of 1743 and 1752 are identical with those of the second, but these editions were not prepared by Linnaeus.

In the fifth and crucial edition (1754, p. 362), Linnaeus treated *Cacalia* of Vaillant and Tournefort as congeneric with *Kleinia* and combined the two under the name *Cacalia*: "CACALIA.\* *Vaill. A. G.* 1719. *Tournef.* 258. *Kleinia edit. prior. Cacalanthemum Dill. elth.* 54. 55. An *Tithymaloides*? *Klein. monagr.* *Porophyllum Vaill. A. G.* 1719. t. 20. f. 39." Most interestingly, the generic description is identical with that of *Kleinia* of the first four editions of *Genera Plantarum*! There is no mention of the tetramerous corolla of *Cacalia alpina* which had appeared in earlier editions under *Tussilago*.

Rydberg argued (*loc. cit.*) that "Linnaeus' description of the genus [*Cacalia*] points to this species [*C. alpina*] especially the description of the style tips: 'Stigmata duo, oblonga, revoluta.' This is characteristic of *Adenostylis alpinus* which on account of its oblong style branches had been placed in the tribe EUPATORIEAE, but which Dr. B. L. Robinson rightly restored to the SENECEONEAE. *C. atriplicifolia* as well as *C. suaveolens* has a true *Senecioid* style, with truncate style-branches." Cuatrecasas further argued, "Among all the species of *Cacalia* in Linné's *Species Plantarum*, *Cacalia alpina* is the only one with elongate, curled stigmas and 4-merous corollas." Cuatrecasas is correct, but Linnaeus's description (1754) of the corollas of *Cacalia* as five-fid and the stigmas as "duo, oblonga, revoluta" does not apply to *C. alpina* but to the species which he had formerly placed in *Kleinia*, a name which he abandoned in favor of *Cacalia* in 1753. Moreover, the description of the corolla and stigmas is precisely the same as in *Senecio* (*Gen. Pl. ed.* 5. 373).

A note under *Cacalia alpina* in *Species Plantarum* (1753, p. 836) reads: "*Hanc speciem genere cum antecedentibus convenire docuit autopsia, hinc genere conjugenda: Cacalia cum Kleiniis.*" In the second edition (1763, p. 1171) this note is clearer and is amplified: "*Hanc speciem genere cum antecedentibus convenire docuit autopsia, hinc genere conjugendae Cacaliae cum Kleiniis. Calyx hujus speciei flosculis 3 s. 4 tantum.*" We translate this to read: "My observation has shown this species to agree generically with the preceding ones; hence the *Cacalias* are to be joined in a genus with the *Kleiniis*. The involucre of this species with only 3

or 4 florets." From this comment and the placement of the species last in the genus it appears that Linnaeus regarded *C. alpina* as somewhat aberrant in, but belonging to, the genus which he had formerly called *Kleinia*. The use of the plural of *Cacalia* also suggests that he had in mind more than one species.

Linnaeus did not change the description of *Cacalia* in the sixth edition of the *Genera*, but the authors of the seventh and eighth editions noted the departures of *C. alpina* from the others of the genus. Reichard (Gen. Pl. ed. 7. 411. 1778) observed, "*C. alpina foliolis calycis conglutinatis corollulisque quadrifidis differt.*" Schreber (Gen. Pl. ed. 8. 545. 1791) included in the description of the corolla "*limbo quadri-f. quinquefido, erecto,*" and Haenke in his edition (Gen. Pl. ed. 8. 709. 1791) had precisely the same description and observation as Reichard. Cuatrecasas (1960, p. 182) attributes a comment to Schreber (1791, p. 545) which we have been unable to locate in the copy available to us: "Cacalia differt a Senecione flosculis quadrifariam scissis."

To return to 1753, *Cacalia* as set forth by Linnaeus in the works which are the starting points for botanical nomenclature has a protologue which is that of *Kleinia* of the first four editions of the *Genera Plantarum*, with the exception of the pre-Linnaean Vaillant and Tournefort references to *Cacalia*, both of which apply to *C. alpina*. *Cacalia alpina* does not agree with the generic description in either corolla or stigmas, but a number of the other species do, among them species currently assigned to *Cacalia* and those removed by Miller to *Kleinia*. It appears that this is but another example of Linnaeus's changing the name of a genus (*Kleinia*) to one which he liked better (*Cacalia*), even though the species which had borne that name historically was somewhat aberrant within an already heterogeneous genus. In the interests of nomenclatural stability, it seems to us most unwise and unwarranted to do anything but to begin the nomenclatural and taxonomic history of *Cacalia* at 1753 and to proceed from that year in the choice of a type species. The species chosen should be in agreement with the protologue and must be one of the ten described in *Species Plantarum* in 1753, taking into consideration those which have been removed to other genera. In reaching the conclusion that *Cacalia hastata* must be the lectotype species, our reasoning follows essentially the same arguments as those succinctly presented by Shinnars (1950).

All of the ten original species have been transferred to one or more other genera at one time or another. The chronological sequence of the more important of these transfers follows:

*C. papillaris*, *C. anteuphorbium*, *C. kleinia*, and *C. ficoides*: Segregated as the genus *Kleinia* by P. Miller (Gard. Dict. Abr. ed. 4. 2: ord. alph. 1754), although the combinations under that genus were not made until much later by Haworth (1812) and De Candolle (1838).

*C. alpina*: Transferred to *Tussilago* L. by Scopoli (Fl. Carniol. ed. 2. 2: 156. 1772) as *T. Cacalia* Scop. (not *T. alpina* L.). Placed in a new genus, *Adenostyles*, by Cassini (Dict. Sci. Nat. Paris 1(Suppl.): 59. 1816).

*C. Porophyllum*: Removed by Cassini (Dict. Sci. Nat. Paris 43: 56. 1826) to *Porophyllum* Guett. as *P. ellipticum* Cass.

- C. suaveolens*: Placed in *Senecio* L. by Elliott (Sketch Bot. S. Carol. & Ga. 2: 328. 1823); later placed in *Synosma* Raf. ex Britton & Brown (Illus. Fl. No. U.S. Canada 3: 474. 1898).
- C. sonchifolia*: Tentatively removed to *Crassocephalum* Moench (= *Gynura* Cass., nom. cons.) by Lessing (Synop. Comp. 395. 1832). Later placed in *Emilia* Cass. by De Candolle as *E. sonchifolia* (L.) DC. ex Wight (Contr. Bot. India 24. 1834).
- C. hastata* L.: Tentatively referred to *Ligularia* L. by Lessing (Synop. Comp. 390. 1832), but the combination under *Ligularia* not made. Later transferred to *Senecio* as *S. sagittatus* by Schultz Bipontinus who united *Cacalia* with that genus (Flora 28: 498. 1845).
- C. atriplicifolia* L.: Transferred to *Mesadenia* Raf. (nom. superfluum = *Arnoglossum* Raf.) by Rafinesque (New Fl. N. Am. 4: 79. 1838). Treated as a *Senecio* by Hooker, who combined *Cacalia* with *Senecio* (Fl. Bor.-Am. 1: 332. 1834).

By the beginning of 1838 only *Cacalia hastata* and *C. atriplicifolia* of the original species had not been transferred formally to other genera. Early in 1838 appeared Volume six of A. P. de Candolle's *Prodromus*, which included a revision crucial in the typification of *Cacalia*. De Candolle divided *Cacalia* into four sections, retaining only three of Linnaeus's original species: *C. hastata* and *C. suaveolens*, which he placed in section *Eucacalia* DC., and *C. atriplicifolia*, which was a member of section *Conophora* DC. Thus, he effectively limited the choice of lectotype to either *C. hastata* L. or *C. suaveolens* L. Since *C. suaveolens* had been transferred to *Senecio* by Elliott (1823), who left *C. atriplicifolia* in *Cacalia*, *C. hastata* becomes the lectotype species. This species is quite in accord with the original description of the genus (Linnaeus, Gen. Pl. ed. 5. 362. 1754), and we can see no reason for choosing another species.

The selection of *Cacalia hastata* as lectotype for *Cacalia* L., primarily on the basis of the removal of the other species to different genera, is in accordance with both the Guide for the Determination of Types set forth in the International Code and the recommendation (7B) that the lectotype should be so selected as to preserve current usage. As so typified, *Cacalia* is a genus of North America and Asia (including easternmost Europe). The question of whether a number of genera should be segregated from *Cacalia* as now circumscribed taxonomically is not yet settled, but no matter what the outcome of future investigations, *Cacalia* as typified by *C. hastata*, will be stable and a minimum of new combinations will have to be made.

We regard the species of *Cacalia* in eastern North America as belonging to two sections: CACALIA, represented in North America by *C. suaveolens* L. and in Asia by *C. hastata* L. and a number of allied species; and CONOPHORA DC., restricted to eastern North America. (Cf. Vuilleumier, 1969.) The pertinent synonymy of these sections is shown below:

*Cacalia* L. Sp. Pl. 2: 834 1753; Gen. Pl. ed. 5. 362. 1754.

#### Sect. *Cacalia*.